• ANNALES CRYPTOGAMICI et PHYTOPATHOLOGICI •

*edited by Frans Verdoorn*

Volume I

# ROOT DISEASE FUNGI

# ANNALES CRYPTOGAMICI et PHYTOPATHOLOGICI

*(incorporating Annales Bryologici)*


*edited by*

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*Wij en konnen den Heer en maker van het geheel Al niet meer verheerlijken, als dat wij in alle zaken, hoe klein die ook in onse bloote oogen mogen zijn, als ze maar leven en wasdom hebben ontfangen, zijn al wijsheit en volmaaktheit, met de uiterste verwondering sien uit steken.*

*Antoni van Leeuwenhoek*

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*WALTHAM, MASS., U.S.A.*

*Published by the Chronica Botanica Company*

# ROOT DISEASE FUNGI

*A Treatise on the Epidemiology of Soil-borne Disease in Crop Plants, and a First Exposition of the Principles of Root Disease Control*

*BY*

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*"Its movements being so little reducible to rule, experience and observation are at fault in endeavouring to explain it, and hence conflicting ideas. This difference perplexes the inquiry, whilst the rapid spread of the pest, and the fear that it will every year encroach upon wider tracts of country, render close observation and study a duty of the utmost importance."*—Report of South Australian Commission on the Take-all Disease of Wheat, 1868.

# PREFACE

*The root-infecting fungi, as an ecological group, afford a wealth of material to the student of evolution; to the plant pathologist, they offer a series of intricate problems in applied biology. In text-books of plant pathology, these and other parasitic fungi are usually grouped, for convenience, taxonomically—an arrangement which tends to obscure the ecological relationship between the fungus and its habitat. I have written this book in order to emphasise the relationship between one such group of plant parasites and its habitat, the soil.*

*Over the surface of the globe, the soil environment of micro-organisms and plants varies less widely than the above-ground environment; especially is this true of cultivated soils. The problems of root disease control in tropical crops are the same in all essential respects as those encountered amongst the crops of temperate regions. Methods of root disease control therefore vary not so much regionally as with the type of cultivation,* viz. *field, plantation, or glasshouse cropping.*

*This book is not intended to be a text-book, and no attempt has been made to deal comprehensively either with all root-infecting fungi, or with the diseases that they cause. Instead, I have focussed attention on a comparatively small number of well-known fungi, causing diseases of notable economic importance. In Chapters 2-8, I have discussed the behaviour of the root-infecting fungi, and attempted to demonstrate certain trends in the subterranean evolution of the parasitic habit. In Chapters 9-15, I have dealt with the principles of root disease control under different types of cultivation.*

*It is difficult to exaggerate my debt to the Editor and Staff of the* "Review of Applied Mycology" *for their excellent abstracts, which have added much to the scope of this undertaking.*

*Finally, I desire especially to thank my colleague, Mr.* F. C. BAWDEN, *for his most generous help in reading and criticising the whole of the manuscript.*

Autumn 1944

ROTHAMSTED EXPERIMENTAL STATION
HARPENDEN, HERTS.

# CONTENTS

Chapter 14



Chapter 15

*Chapter 1*

# INTRODUCTION

The history of root disease investigation falls into a series of well-marked though overlapping phases, and may be considered to have started with the second half of the nineteenth century. During these fifty years, the economic importance of root diseases was increasingly appreciated by growers and professional botanists alike, but many and varied were the hypotheses put forward in explanation of such diseases; as THAXTER (1891) remarked of potato scab: "It is a well-known fact that the theories and explanations which have been advanced to account for certain diseased conditions of the surface of potato tubers generally known as scab are nearly as numerous as the experimenters who have studied the disease." Especial weight was given not only by farmers but also by men of science to the non-living factors of the environment as a probable cause of root disease; either soil or season might be blamed, though insect pests were sometimes held responsible. Parasitic origin of disease is a commonplace to us today, but to botanists of the nineteenth century, it was a novel and even a startling idea; it is not surprising, therefore, that farmers were at first unwilling to abandon their former hypotheses of soil, climate or insect pests as responsible for root disease in their crops, in favour of hypotheses postulating a microscopic parasite, which they were often unable even to see.

Rules of proof were formulated by KOCH (1882), through the application of which the connection between a bacterial parasite and the disease which it caused in man or animal might experimentally be established. These rules are: (1) constant association of the organism with the disease, (2) isolation of the organism in pure culture, (3) reproduction of the disease by inoculation with the pure culture of the organism, (4) re-isolation of the organism from the inoculated diseased host, and identification of it with the original inoculant. Plant pathologists have generally accepted KOCH's postulates as binding on them, too, though with obligate parasites such as *Plasmodiophora brassicae,* which cannot be cultured on artificial media, the procedure cannot be followed in full. Nevertheless, strict compliance with these rules of proof was by no means universal amongst the early investigators of root diseases. The first rule was always followed, but the second and third rules were not, naturally-infected host tissues often being substituted for pure cultures in inoculation experiments; as remarked above, this procedure was unavoidable where an obligate parasite was concerned. The fourth rule was most commonly neglected of all. Fortune favoured many of the earlier investigators, inasmuch as they discovered the primary parasite responsible for a root disease in spite of incomplete compliance with KOCH's postulates.

This combination of good fortune with intuition, as a supplement to scientific method, has been rewarded by the fame always attaching to discovery, however made!

One of the first soil-borne diseases to be correctly attributed to the activity of a parasitic fungus was stem canker and tuber scurf of potatoes, which KÜHN (1858) in Germany showed to be due to infection by *Rhizoctonia solani.* Not long afterwards, REINKE and BERTHOLD (1879) showed that a wilt of potatoes in the same country was due to infection by another fungus, *Verticillium albo-atrum.* Just before REINKE and BERTHOLD's discovery, HARTIG (1873), the well-known German forest pathologist, had shown *Armillaria mellea* to cause a serious root disease in forest trees. These early discoveries by German investigators reflect the well-known pre-eminence of Germany at that time in the sciences of botany and plant pathology. Then, however, the famous Russian mycologist, WORONIN (1878), published his discovery of *Plasmodiophora brassicae* as the cause of clubroot in crucifers, a widespread disease which had been only too well-known all over Europe for many years previously. Then PRILLIEUX and DELACROIX (1890) correctly proclaimed that *Ophiobolus graminis* was at least one of the parasites causing foot rot or "piétin" of wheat in France; not long afterwards, McALPINE (1904) declared that the two diseases familiar to Australian farmers as "take-all" and "whiteheads" were in reality different phases of the same disease, due to infection by *Ophiobolus graminis,* the cause of the "piétin" in France. In the U. S. A., PAMMEL (1890) was the first investigator to assign the cause of Texas root rot of cotton to infection by *Ozonium auricomum;* the validity of PAMMEL's discovery was not affected by SHEAR's (1907) transfer of the cotton root rot fungus to a new species, *O. omnivorum.* With DUGGAR's (1916) discovery of a sporing stage of this fungus, the name was changed once more to *Phymatotrichum omnivorum,* by which the cotton root rot fungus is still known. At about the same time, another American investigator, THAXTER (1891, 1892), demonstrated that *Oospora scabies* was the cause of potato scab; this organism is now classified not with the Fungi, but with the Actinomycetes, and its name has therefore been changed to *Actinomyces scabies.* The cause of another soil-borne disease well-known at that time in the U. S A., black root rot of tobacco, was discovered not there but in Italy by PEGLION (1897), who determined it (albeit not quite correctly) as *Thielavia basicola;* the tobacco root rot fungus is now known as *Thielaviopsis basicola.* Somewhat later, investigators turned their attention to the root diseases of tropical crops; RIDLEY (1904) determined *Fomes semitostus* (now corrected to *F. lignosus*) as the cause of white root disease of rubber in Malaya, whilst some twelve years later BELGRAVE (1916) ascribed red root disease of the same plant to another hymenomycete (now known as

*Ganoderma pseudoferreum*). Credit for discovering the parasite responsible for the widespread Panama disease of bananas should go to the well-known American plant pathologist, ERWIN F. SMITH (1910), who obtained pure cultures of a fungus which he named *Fusarium cubense* (now re-classified as *F. oxysporum cubense*) from tissues of wilted banana plants sent from Cuba. He induced symptoms of disease by inoculation of this fungus into glasshouse-grown bananas at Washington, D. C. Most of the credit for establishing *F. oxysporum cubense* as the cause of Panama disease has rightly gone, however, to BRANDES (1919), who in 1915, in ignorance of the report by E. F. SMITH, set up extensive inoculation experiments in Porto Rico to determine whether this fungus was the responsible pathogen; in BRANDES' experiments, KOCH'S rules of proof were rigidly followed in every particular.

It is no matter for surprise that the parasitic origin of most soil-borne diseases, at first slow to gain recognition, should later have come to be enthusiastically accepted by botanists and plant pathologists, to the exclusion for some years of other considerations. The very name of mycologist, by which some plant pathologists are still officially known, is eloquent of this excessive preoccupation with the parasite. Control measures were directed particularly towards elimination or inactivation of the parasite, whether in the soil or in the tissues of the host. This is not to say that plant pathologists during this period entirely neglected the possibility of indirectly controlling soil-borne diseases, through the influence of soil conditions. HALSTED (1900), for instance, reported that the clubroot disease of crucifers was favoured by acid soils, whereas potato scab was encouraged by alkaline soils.

At length, however, investigators began to realise that the soil environment exercised a profound effect upon the development of most soil-borne diseases, and that the suitability or not of the environment for development of disease in the plant might be a factor as important as the presence or absence of the parasite. The credit for bringing about this change of view must go especially to the Wisconsin school of investigators, led by L. R. JONES; a summary of this work is given by JONES *et al.* (1926) in their outstanding monograph on the relation of soil temperature to plant disease. Particular attention was paid by the Wisconsin workers to the effect of soil temperature upon soil-borne diseases, and a technique for accurate control of soil temperature under experimental conditions was evolved. The American investigators took full advantage of the opportunity which climatic variations of continental extent in the U. S. A. afforded them, in correlating incidence of disease with soil and air temperatures in different regions.

**Microbiological Equilibrium of the Soil:** — The importance of the non-living factors of the soil and aerial environment in their effect upon the development of soil-borne disease became well established by work at Wisconsin and elsewhere. In the late twenties of the present century, another factor of the soil environment, of profound importance, at last received recognition, when it came to be realised that development of a soil-borne disease might be affected not only by the behaviour of the particular parasite concerned, but also by that of other micro-organisms as well. Commenting upon the control of potato scab by green manuring with grass cuttings, reported by MILLARD (1921), SANFORD (1926) was the first to suggest that such control might be brought about through the antagonism to *Actinomyces scabies* of saprophytic species of bacteria developing on the decomposing green manure. MILLARD and TAYLOR (1927) later showed that the development of scab on potatoes grown in sterilised soil inoculated with *A. scabies* could be reduced by simultaneous inoculation of the soil with *A. praecox,* an obligate saprophyte of a more vigorous habit of growth.

In nature, the host-parasite relationship must be affected by the biotic as well as by the non-biotic factors of the environment. In infected roots, the fungus causing the disease is rapidly followed into the host tissues by other micro-organisms, with which it must thereafter be associated. The pure-culture method of experimentation, as postulated by KOCH, is essential for solution of the original problem, *i.e.* determination of the primary parasite responsible for production of disease in the host. Once this question has been settled, however, experimentation should no longer be restricted to work with pure cultures of the parasite introduced into sterilised soil; some experiments, at least, should be carried out in natural unsterilised soil, under conditions permitting full play of the microbiological factor. A timely warning concerning the false conclusions which might be derived from such methods of pure culture experimentation was voiced by FAWCETT (1931) in his Presidential Address to the American Phytopathological Society; FAWCETT suggested that experiments with cultures of single micro-organisms should be supplemented by others in which known mixtures of micro-organisms were employed.

Attention was also drawn to the importance of the microbiological factor in the soil environment of the root-infecting fungi by the experiments made with cereal root rot fungi by certain Canadian investigators, to whom particular credit is due. For the purpose of making pot and field experiments with one of these fungi, it was customary to culture the organism upon some organic medium, such as cooked wheat kernels, a mixture of oats and pearl barley, oat hulls, or a mixture of soil or sand with cornmeal, etc. The infected material was buried in the experimental soil, often in rather large quantities. Such

inoculum did not prove very satisfactory, however, owing to its rapid deterioration in virulence; after a few months, inoculated soils often proved completely harmless to cereal seedlings planted therein. Since this deterioration was more rapid in field soil than in sterilised or partially sterilised soil in pots, SANFORD and BROADFOOT (1931) suggested that it was due to the operation of microbiological antagonism upon the pathogenic inoculum. They found that infection of wheat seedlings by *Ophiobolus graminis* was completely suppressed by the antagonistic action of a number of fungi and bacteria, not only by the living cultures, but also, in many instances, by their culture filtrates as well. HENRY (1931) found that the growth of *Helminthosporium sativum* upon sterilised soil in small flasks might be completely suppressed by the addition of very small amounts of unsterilised soil, or by simultaneous inoculation with a number of other fungi and bacteria, so that no infection resulted when wheat seeds were inoculated with the contents of the flasks in small pots. BROADFOOT (1933*a*) showed that infection of wheat seedlings by *Ophiobolus graminis,* initially much less in unsterilised than in sterilised soil, fell off markedly with the progress of recolonisation of the sterilised soil by the returning microflora. MORITZ (1932) observed that the severity of the take-all (*O. graminis*) disease of wheat on three German soils could be inversely correlated with the "protective" action of the general soil microflora, which was estimated by comparing infection in the unsterilised soil with that obtained in the sterilised soil. The interaction of microbiological antagonism with temperature was first demonstrated by HENRY (1932) for wheat seedling infection by *O. graminis*. HENRY'S findings were confirmed by GARRETT (1934*a*), and extended to other cereal foot rot fungi (GARRETT, 1934*b*). Rising soil temperature was found by these authors to increase microbiological antagonism to the parasitic fungus; the fundamental effect of high soil temperature in accelerating infection could be seen under sterile conditions, but it was masked in the presence of other soil micro-organisms by their inactivation of the pathogen inoculum, which increased with rising temperature. From these and later experiments, it appeared that total exclusion of the microbiological factor from all experiments on soil-borne diseases was undesirable, as being too far removed from natural conditions in the field; still further removed from natural conditions, however, were those experiments in which this factor had been unduly emphasised, *i.e.* by the use as inoculum of fungal cultures on rich media containing unassimilated carbohydrates and other nutrients, mixed in high proportion with the soil.

In sterilised soil, with or without supplementary carbohydrates or other organic nutrients, a much simplified microflora in the presence of relatively high nutrient concentrations is obtained. These conditions approach those of experiments on plates of nutrient agar, in which two

selected fungi or other micro-organisms are grown in juxtaposition. In such plate cultures, striking demonstrations of antagonism have been reported by many investigators, for an account of which the reviews of WAKSMAN (1937, 1941), PORTER and CARTER (1938), WEINDLING (1938) and D'AETH (1939) should be consulted. Not merely antagonism, but even actual parasitism of one micro-organism upon another has been demonstrated in such agar plate experiments. A noteworthy example is the parasitism of *Trichoderma lignorum* upon *Rhizoctonia solani* and other fungi; the mechanism of this parasitism has been brilliantly elucidated by the researches of WEINDLING and his collaborators (WEINDLING, 1932, 1934, 1937, 1941; WEINDLING and EMERSON, 1938; WEINDLING and FAWCETT, 1936). In so far as conditions in sterilised soil, *viz.* a much simplified microflora and abnormally high nutrient concentration, repeat those of the agar plate, similar results have been obtained; witness HENRY'S (1931) demonstration that growth of *Helminthosporium sativum* on sterilised soil might be completely suppressed by the addition of a mere pinch of unsterilised soil, and a similar demonstration by MITCHELL *et al.* (1941) with *Phymatotrichum omnivorum* on a substrate of sterilised cotton roots. In natural soil, on the other hand, the microflora is far more complex, and the concentration of free nutrients is very much lower. The special conditions favouring development of antagonism, or parasitism of one micro-organism upon another, on the agar plate and in sterilised soil are therefore absent in unsterilised or natural soil. This may be concisely expressed by saying that *natural soil is biologically buffered.* For this reason, "biological control" has often failed to fulfill in field trials its extravagant promise on the agar plate or in pots of sterilised soil.

The most important effect of the microbiological factor upon the root-infecting fungi is probably to be found not so much in restriction of their parasitic activity as in curtailment of their saprophytic existence. From the ease with which most root-infecting fungi could be cultured for indefinite periods as saprophytes on artificial media, it was often formerly supposed that they might persist indefinitely in the soil, existing and even spreading upon the organic matter of the soil. Such a conclusion ignored, of course, the very effective control of most soil-borne diseases by the practice of crop rotation. It was undermined by WAKSMAN'S (1917) discovery that there is a cosmopolitan microflora of soil-inhabiting fungi, composed of regular saprophytes; amongst this flora of *soil inhabitants,* other fungi were present as exotics, or *soil invaders.* WAKSMAN'S conception was applied by REINKING and MANNS (1933, 1934) and REINKING (1934) with conspicuous success to their conclusions concerning the distribution of species of *Fusarium* in the soils of Central America. Certain *Fusarium* spp. were present in all, or nearly all, the soils examined, and were

designated as *soil inhabitants;* other *Fusarium* spp. were present in the soil only in close association with tissues of their host plants, and eventually disappeared, thus meriting WAKSMAN's term of *soil invaders.* This distinction made by REINKING and MANNS between saprophytic and parasitic species of *Fusarium* was later extended by GARRETT (1938*a*) to differentiate between two contrasting types of behaviour amongst root-infecting fungi in general.

**Root Disease Control:** — Some consideration must now be given to the application of these discoveries to the problems of root disease control in crops. Certain measures of root disease control are applicable to root diseases of all crops in all countries, and some of these, indeed, to almost all diseases of crops. Such, for example, are the production of disease-resistant or disease-immune varieties of the crop plant, and the practice of crop sanitation, *e.g.* prevention of disease introduction through infected planting material, etc. Little further space will be devoted to such measures, important as they are, in the following pages, because they belong to the province of plant pathology in general, rather than to that of root disease control in particular. Special control measures in use against root diseases are best considered in relation to the type of crop, *viz.* field crops, plantation crops, and glasshouse crops.

The root diseases of field crops are controlled by crop rotation, by application of the principles of plant sanitation to the disposal of infected residues, and by checking the development and spread of root disease under the growing crop. Crop rotation is the oldest and most effective method of root disease control in field crops; its effectiveness is least against those diseases caused by fungi forming long-lived resting spores or sclerotia at the conclusion of periods of parasitic activity. A noteworthy study of the relation between length of crop rotation essential for root disease control and survival of the causal organism, *Phymatotrichum omnivorum,* in the soil was carried out by ROGERS (1937), working on cotton root rot in Texas. Recent evidence, presented by BOSE (1938) in India and by HILDEBRAND and WEST (1941) and RICHARDSON (1942) in Canada, suggests that certain crops in a rotation may depress the incidence of soil-borne disease in a following crop more than others, even though all such preceding crops are alike in being non-susceptible to attack by the particular parasite or parasites concerned. A notable advance in crop sanitation was made by KING *et al.* (1934*a*) and KING (1937) when they demonstrated that losses due to cotton root rot (*P. omnivorum*) in continuous cotton under irrigation in Arizona could be greatly reduced by incorporation of organic material in the soil some months before cotton was sown. This reduction in disease was tentatively attributed by KING *et al.* to biological control of *P. omnivorum* by saprophytic soil

micro-organisms developing on the added organic material; MITCHELL *et al.* (1941) and CLARK (1942) have obtained fresh evidence in support of this hypothesis, and have also shown that sclerotia of *P. omnivorum* may be induced to germinate by the presence of decomposing fresh organic material in the soil. It seems likely, too, that the plant nutrients liberated during decomposition of the green manure may enhance the resistance of the cotton plant to this disease (JORDAN *et al.*, 1939).

Variation in the incidence of soil-borne diseases with soil conditions is now well known, and has been exploited in a variety of ways. In the field, some control of soil temperature, at least during the early stages of crop growth, can be secured by variation in planting time. Thus RICHARDS (1921, 1923*a*) working in Utah showed that the incidence of stem canker (*Rhizoctonia solani*) of potatoes, a disease favoured by low soil temperatures, could be greatly reduced by delaying the date of potato planting. Direct control of soil moisture is impossible in the field except under irrigation; in Egypt, JONES and SEIF-EL-NASR (1940) demonstrated a striking control of certain cereal smut diseases through very shallow sowing in very wet soil. Soil aeration can be directly controlled, to a considerable extent, by cultivation; in Australia, the preparation of a very firm seed-bed for wheat was found many years ago by pioneer farmers to be an effective means of reducing the ravages of the take-all (*Ophiobolus graminis*) disease. The effect of soil acidity in controlling scab (*Actinomyces scabies*) of potatoes, and of soil alkalinity in controlling clubroot (*Plasmodiophora brassicae*) of crucifers is well known. The control of scab by green manuring (MILLARD, 1921) is surprisingly effective in smallholdings, where very large amounts of fresh, chopped-up organic matter, such as grass cuttings, can be thoroughly incorporated with the soil. The concentration of plant nutrients in the soil may have a paramount effect upon the occurrence of certain soil-borne diseases, such as browning root rot (*Pythium* spp.) of cereals in Canada, which can be effectively controlled by application of phosphate (VANTERPOOL, 1940*b*).

In tropical plantation crops, special care was formerly advised in eradicating all sources of root disease inoculum after clearing virgin jungle or an old plantation site, since at no subsequent time in the life of the plantation would a similar opportunity be offered. Conscientious adoption of this advice entailed great, and expensive, labour in the excavation of buried roots before planting up. The second line of defence against root disease in tropical plantation crops lay in the practice of trenching, to stop advance of the root disease fungi, some of which were supposed to spread through the soil as free-growing mycelium. A good account of the earlier methods of root disease control in rubber plantations is given by PETCH (1921). Principles

of root disease control in rubber plantations were later revolutionised through the brilliant investigations of NAPPER (1932-40) at the Rubber Research Institute of Malaya; a well-documented history of rubber root disease investigations has been compiled by SHARPLES (1936). By NAPPER's method, a minimum of clearing is carried out on a virgin jungle site in preparation for rubber, but a collar and proximal root inspection of all the young rubber trees is made at intervals of a few months by gangs of labourers trained to recognise the mycelia of the root disease fungi. When the mycelium of one of the root parasites is discovered, at such a routine inspection, on the proximal part of a tap or lateral root, the epiphytic mycelium is peeled off, and the root lightly rubbed with copper sulphate solution; the infection is traced to its source, a piece of infected jungle timber, and both infected root sections of the young rubber tree and the source of infection are removed and destroyed. The method depends for its success upon the fact that the mycelia of these root parasites of the rubber tree are epiphytic for some distance ahead of penetration; that of *Fomes lignosus,* the most important root parasite of young rubber on jungle sites, is epiphytic for as much as 5-15 feet ahead of penetration. A similar method can be used for eradication of root disease in young rubber on the site of former plantations, but if root disease has been severe in the old stand, a preliminary excavation of infected roots is advised before planting.

Roots of jungle or plantation trees infected by root disease before felling are not the only source of danger to the young plantation crop, however; the act of felling may so lower the natural resistance of the roots as to render them susceptible to rapid infection by a parasite to which they were formerly somewhat resistant. This fact was first demonstrated by LEACH (1937, 1939), working with *Armillaria mellea* on tea in Nyasaland; this fungus attacks few trees in the standing jungle, but develops freely as a parasite in the roots of many species once the tops have been felled. LEACH further demonstrated that if the trees were killed by ring-barking some time before felling, their roots were invaded not by *A. mellea,* but by harmless saprophytes, such as *Rhizoctonia bataticola.* LEACH's discoveries will undoubtedly exercise a profound effect upon the development of methods for root disease control in tropical plantation crops. NAPPER (1939, 1940) has since shown that a substantial proportion of the infections by *F. lignosus* in young rubber plantations must be due to infected roots of old jungle or plantation trees which are healthy at the time of felling, but which rapidly become infected by *F. lignosus* after felling, consequent upon the sharp lowering of host resistance. NAPPER found that killing of the trees or stumps by injection with sodium arsenite before or immediately after felling appeared to eliminate such post-felling infection of the roots by *F. lignosus;* injection by sodium arsenite in Malaya thus fulfilled the same function as ring-barking in Nyasa-

land. The practical importance of these discoveries is too obvious to require further emphasis.

The greater degree of control over soil and aerial environment possible in glasshouse practice should permit the development of more direct methods of root disease control than is possible in the field. A good example of such is furnished by BEWLEY's (1922) method of controlling the wilt of tomatoes due to *Verticillium albo-atrum* by raising glasshouse temperature to a level exceeding 25°C. Control of root diseases under intensive glasshouse cropping is chiefly effected, however, by partial sterilisation of the soil through heat or chemicals. Such partial sterilisation, which has become a routine in good commercial glasshouse practice, greatly benefits crop growth, apart from its valuable effect in controlling root diseases and pests. The benefits of partial sterilization were discovered independently by GIRARD (1894) in France and by OBERLIN (1894) in Alsace, using carbon disulphide; DARBISHIRE and RUSSELL (1907) later demonstrated that heat treatment of soil produced a similarly beneficial effect upon crop growth in "sick" glasshouse soils. At present, heat is more commonly employed for soil sterilisation in glasshouses than are chemicals, though a cheapening of antiseptics in present use, or the discovery of cheaper or still more effective ones, may reverse this situation. It seems safe to predict, however, that treatment of soil by fungicidal chemicals is unlikely to find any general application outside its present limited sphere of usefulness, *viz.* in glasshouses, in nursery beds, and in intensive or market garden cropping. Some development in the "placement" of soil fungicides can be expected, in parallel with the development now proceeding in "placement" of artificial fertilisers. By the placement method, one of the chief difficulties involved in fungicidal treatment of soil, *viz.* the great bulk of soil to be treated, is evaded. A good example of this procedure is afforded by PRESTON's (1928, 1931) use of mercuric chloride for watering in young cabbage plants at transplanting, in soils infected by the clubroot parasite (*Plasmodiophora brassicae*). A further development along such lines may be the use of soil fungicides in conjunction with mechanical planters and transplanters, as in the well-known formalin drip treatment for control of onion smut, originally devised by SELBY (1902), and greatly improved by ANDERSON and OSMUN (1923).

*Chapter 2*

# PARASITIC SPECIALISATION IN THE ROOT-INFECTING FUNGI

When a plant dies, its roots are quickly invaded by various soil micro-organisms, prominent amongst which are species of soil fungi. The competition between members of the soil microflora for colonisation of this freshly opened substrate is intense, but the results are by no means determined by chance; the organisms which become dominant colonists are those best fitted to decompose that particular substrate under those particular environmental conditions. With the progress of colonisation and decomposition of the substrate, the habitat is changed, so that other organisms become dominant in their turn, and so there is a tendency for a *succession* of micro-organisms to develop. The decomposition of dead root tissues in the soil is thus merely a particular instance of a general phenomenon well known to plant ecologists.

This succession of micro-organisms developing in dead root or other plant tissues buried in the soil has been studied, either deliberately or incidentally, by a number of workers. The plant tissues have usually been surface sterilised, washed, and then plated out on a nutrient agar. The number of fungus species forming colonies on the agar plate may constitute only a small fraction of the total number engaged in decomposition of the plant tissues; the colony-forming species must be those that are best suited by the nutrient agar substrate. The particular species forming colonies must be determined not only by the nature of the nutrient agar substrate, but also by other conditions of incubation, such as that of temperature; WALKER (1941), moreover, has demonstrated that the choice of surface sterilising agent may strongly influence the results. WALKER buried short lengths of fresh wheat straw in the soil, and took samples for surface sterilisation and plating-out at regular intervals. The dominant fungi producing colonies on the agar plates were *Fusarium culmorum* and *Penicillium* spp.; the ratio between the numbers of *F. culmorum* colonies and those of *Penicillium* colonies developing from any sample of straws varied within very wide limits according to the type of surface sterilising agent employed and the time of treatment. *F. culmorum,* a fungus of a vigorous and rapid habit of growth, showed low resistance to the action of the more severe sterilising agents, such as mercuric chloride and silver nitrate, but developed better after surface sterilisation of the straws with calcium hypochlorite, a mild sterilising agent, and best of all after a mere washing in sterile water. *Penicillium* spp. were apparently crowded out by the more vigorous growth of *F. culmorum* after these mild treatments of the straws; on the other hand, they were very tolerant of the more severe surface sterilising agents, mercuric chloride

and silver nitrate, and after the longer period of treatment were often the only organisms developing on the plates.

Further to pursue the concepts of plant ecology, we may recall the development in certain plants of an ability to colonise certain virgin habitats unfavourable to general plant growth. The most frequently quoted examples of such habitats are sand dunes, shingle banks, and bare rock faces. By the evolution of a specialised growth habit, such plants are considered to have *escaped* from the intense competition characteristic of habitats more favourable to the development of vegetation. *Amongst the soil fungi, this role of escapers has been taken by the root-infecting fungi, which have developed ability to open up and colonise a habitat not available to saprophytic fungi.* To continue the analogy with above-ground plant ecology, we may further recall that in due course the primary colonisers of a sand dune, shingle bank or bare rock face so change the habitat that it permits growth of a wider range of species, with the result that the primary colonisers are gradually ousted and finally disappear completely. In the same way, once a root-infecting fungus has opened up a new habitat, the plant root, it is rapidly followed by other soil micro-organisms. The root-infecting fungus obtains, however, an initial advantage in colonisation which it may retain for longer than was formerly supposed, from results of attempts to isolate it on the culture plate. It is well known that attempts to isolate a root-infecting fungus from diseased tissue, by surface sterilising selected portions of tissue and plating-out on the surface, of nutrient agar, often give disappointing results. This is due to the fact that the nutrient agar plate is a selective medium, not for the primary plant parasite, but for the saprophytes which are its co-habitants in the infected tissues.

Investigators studying the survival of parasitic fungi therefore now generally employ the ideal selective medium, *i.e.* a host plant of the particular fungus concerned. Examples of this technique are furnished by the work of TAUBENHAUS and EZEKIEL (1930*b*) with *Phymatotrichum omnivorum,* of PADWICK (1935), GARRETT (1938*b*), and FELLOWS (1941) with *Ophiobolus graminis,* of THUNG (1938) with *Phytophthora parasitica* var. *nicotianae,* of GIBBS (1938) with *Phoma lingam,* of NAGEL (1938) with *Cercospora beticola,* and of MATZULEVITCH (1936) with *Urocystis cepulae.* In their studies of the root rots of strawberry and tobacco in Ontario, HILDEBRAND (1934), KOCH (1935), and HILDEBRAND and KOCH (1936) have endeavoured to overcome this short-coming of the isolation plate technique by supplementing it with direct microscopical study of the succession of micro-organisms developing in the diseased roots. Presumably, it should be possible to obtain a complete picture of the succession of fungi in such diseased plant tissues by employing a sufficient number of selective isolation media (in the widest sense of this term); as the number of

specific isolation techniques approached the number of fungi involved, so the investigator's knowledge of the succession should approach totality.*

**Soil-inhabiting and Soil-invading Fungi:** — Serious study of the fungus flora of the soil may be said to date from WAKSMAN'S (1917) postulate that there is a definite fungus flora of the soil. From his examination of the fungi found in 25 different soils collected from widely separated regions of the North American continent, and from the Hawaiian Islands, and from the results of European investigators, WAKSMAN concluded that the basic fungus flora of the soil was essentially cosmopolitan, though the relative importance of different groups might vary with latitude and soil type. Thus soils of the northern latitudes were characterised by abundance of *Mucorales* and *Penicillia,* whilst *Aspergilli* were predominant in the warmer soils. Again, the genus *Trichoderma* was found especially in acid soils (*e.g.* forest soils) and in waterlogged soils. As a result of this study, WAKSMAN introduced the fundamental conception of a basic cosmopolitan fungus flora of *soil inhabitants,* amongst which were to be found exotic fungi or *soil invaders.* This conception of WAKSMAN'S was applied by REINKING and MANNS (1933, 1934) and REINKING (1934) to their findings on the distribution of *Fusarium* spp. in the soils of Central America. As the result of a very large series of isolations from soils, these authors concluded that the tropical American soil *Fusaria* could be divided into two groups, *soil inhabitants* and *soil invaders.* The *soil inhabitants* were those species of *Fusarium* found in all, or nearly all, of the soils examined, and were hence regarded as common soil saprophytes. Certain other species, on the other hand, were found to have only a local distribution, and this distribution was further found to coincide with the presence, or past presence, of the appropriate host plant. With the death of the host plant, the numbers of such a species gradually dwindled, until it disappeared from the soil, and was hence designated a *soil invader.*

This conception of *soil inhabitants* and *soil invaders* was in turn employed by GARRETT (1938*a*) to distinguish between two contrasting types of behaviour amongst the root-infecting fungi, as follows: "The *soil inhabitants* are considered to be primitive or unspecialised parasites with a wide host range; these fungi are distributed throughout the soil, and their parasitism appears to be incidental to their saprophytic existence as members of the general soil microflora. The *soil invaders,* to which class the majority of the root-infecting fungi seem to belong, are more highly specialised parasites; the presence of such fungi in the soil is generally closely associated with that of their host plants. In the continued absence of a host plant, such fungi die out in

* Any other effects of such an investigation upon the mind of the investigator are irrelevant to the present discussion.

the soil, owing to their inability to compete with the soil saprophytes for an existence on non-living organic matter. This close association between the *soil invaders* and their host plants thus seems to be enforced by the competition of the general soil microflora."

Any consideration of the qualifications of a particular fungus for its role of a *soil inhabitant* involves recognition of the fact that two factors, of a spatial and a temporal nature, respectively, are concerned. By the spatial factor is implied the number of kinds of plant tissue, or other substrate, which the fungus can colonise; the species of plant, the part of the plant, its age and other causes of variation in tissue composition must all affect not only the rate and course of decomposition in the soil (WAKSMAN, 1931) but also the species of decomposing micro-organisms. By the temporal factor is meant the average period for which the fungus can actively maintain itself on a substrate, during the passage of that substrate from the virgin condition to that of relatively inert soil humus. To take an extreme instance, a root-infecting fungus which was a truly omnivorous plant parasite could certainly be regarded as a *soil inhabitant,* even if its powers of survival as a saprophyte were strictly limited, because at almost all times and in almost all places it could find a substrate. With a fungus of more restricted host range, however, the ability to function as an active saprophyte for a longer period in the decomposing plant tissues becomes correspondingly more important. The development of long-lived resting spores and sclerotia by root-infecting fungi may be regarded as an example of one way by which the disadvantage of nutritional specialisation has incidentally been overcome.

**Mycorrhizal Fungi:** — If symbiosis be regarded as the evolutionary end-point of the parastic habit, then the mycorrhizal fungi must be regarded as the most highly specialised of all the root-infecting fungi. This group of fungi has stimulated continuous interest, and not a few controversies, amongst mycologists ever since the discovery of the mycorrhizal habit in plants. The work of the earlier investigators has been discussed by RAYNER (1927), in her monograph on mycotrophy in plants. More recently, BURGES (1936) has published a concise but comprehensive, and commendably objective, review of the whole subject. Two groups of mycorrhizal fungi are usually distinguished; the *ectophytes,* which develop mainly externally, forming a fungus mantle around the host roots, and the *endophytes,* which develop inside the host tissues. The differences between ectophytic and endophytic mycorrhizas have been lucidly summarised by RAYNER (1939), in the following paragraph: "It is still convenient to classify mycorrhizas into two groups, the extreme types in which show marked structural differences, correlated with the distribution and character of fungus infection. The *ectotrophic* mycor-

rhizas of most trees and shrubs are readily recognisable as distinct from ordinary rootlets; a sheath of mycelium is formed about the tip and younger part of the emerging rootlet and the hyphae composing it extend inward, forming an intercellular network between the cortical cells known as the 'Hartig net'. In *endotrophic* mycorrhizas, a more or less extensive distribution of intercellular and intracellular mycelium within the root is associated with a variable but usually scanty development of hyphae on the surface. In general, endotrophic mycorrhizas resemble ordinary roots in external appearance, although slight modifications such as irregularities of diameter or differences in opacity of the tissues may betray their character to the experienced observer." RAYNER goes on to point out that the distinction between these two types of mycorrhiza is an artificial one, and can be condoned only on grounds of convenience; intermediate types are now known. The association of the ectophytes with their host root may be conditioned by root excretions from the host; MELIN (1925) demonstrated the excretion of phosphatides by the roots of various forest trees, and showed that these stimulated the development of the mycorrhizal fungi.

Evidence for an obligate mycotrophic habit is strongest in the case of certain species of forest trees forming ectophytic mycorrhiza. Foresters have frequently experienced difficulty in establishing exotic coniferous trees; lack of success has usually been associated with absence of typical mycorrhiza formation by the trees. Inoculation of nursery beds with soil taken from under a vigorous stand of the same species of tree has frequently changed failure into success, and the young trees have grown away well in the inoculated soil. RAYNER (1938) has summarised information collected by the Imperial Forestry Institute of Oxford on the use of soil or humus inoculum as an aid to establishment of exotic species of forest trees; the empirical use of such inoculum appears to be widespread, and to give satisfactory results in the majority of trials.

HATCH (1937) has recently published substantial experimental evidence in support of STAHL'S (1900) hypothesis that ectophytic mycorrhizal fungi facilitate absorption of mineral salts by their hosts, especially in infertile soils. He demonstrated a negative correlation between production of mycorrhizae by pine seedlings and the availability of mineral salts in a number of forest soils. In his experiments, mycorrhizae were most abundantly produced under shortage of available nitrogen, phosphorus, potassium or calcium, or under lack of balance between these nutrients. Hatch experimentally demonstrated striking increases in growth and nutrient absorption by seedlings of *Pinus strobus* in a prairie soil after inoculation with pure cultures of appropriate mycorrhizal fungi. HATCH'S observations have been confirmed and extended by ROUTIEN and DAWSON (1943), using an artificial soil compounded of pure quartz sand and a purified colloidal clay.

This artificial soil possessed base exchange properties, and its content of available nutrient ions could be experimentally varied within wide limits. Working with this artificial soil, ROUTIEN and DAWSON found that substantial growth and salt absorption by *Pinus echinata* took place even in the absence of mycorrhizae at the higher levels of base saturation of the soil. But if absorption of nutrients was impeded by replacing the nutrient ions with adsorbed hydrogen ion, then formation of mycorrhizae substantially increased growth and salt uptake by the pine seedlings. HATCH has stressed the increase in total absorbing surface resulting from conversion of short roots into mycorrhizae; ROUTIEN and DAWSON observed that development of such short roots into mycorrhizae doubled or even quadrupled production of respiratory carbon dioxide. They therefore concluded that mycorrhizae increased the salt-absorbing capacity of the roots chiefly by adding to the supply of exchangeable hydrogen ion, derived in part at least from respiratory carbonic acid.

Infection by the appropriate endophyte was formerly thought to be essential for germination of the seed in many species of the *Ericaceae* and *Orchidaceae;* evidence for and against this view has been summarised by BURGES (1936), who states: "RAYNER (1929), as the result of her pure culture experiments, concludes that, unless the seedlings of *Calluna vulgaris* were infected by the endophyte, 'arrest of growth and the inevitable symptoms of malnutrition' followed. This result was in discordance with those of CHRISTOPH (1921) and KNUDSON (1929), who considered that infection was not essential. In a later paper KNUDSON (1933) records the result of his reinvestigation of the problem in the light of RAYNER'S criticisms of his previous technique, and has shown that *Calluna* seedlings can develop normally without the endophyte. FREISLEBEN (1934) has reached a similar conclusion in respect to the genus *Vaccinium.*" In a later paragraph concerned with mycotrophy in seedling orchids, BURGES comments: "It used to be thought that orchid seedlings were unable to germinate and grow on their own account. BERNARD (1904) showed that if the endophytes were added to the cultures growth frequently followed. KNUDSON (1927) has extended this work and has shown that the important feature is not the penetration of the orchid by the endophyte, but the bringing of organic material into solution. For example, on a medium containing starch, the carbohydrate is unavailable to the orchid. If the fungus present causes hydrolysis of the starch, some of the resulting sugars, once in solution, are utilised by the orchid, which is then able to establish itself and later may become independent of this auxiliary food supply. If the organic material were supplied in solution, *e.g.* as fructose, no fungal agent was required. He further showed that other fungi such as *Phytophthora* could replace the endophyte and bring the organic material of the medium into solution.

The fungi also caused a change in the hydrogen-ion concentration of the medium. This on its own did not lead to germination, yet it was shown to be a contributory factor. Other workers have also shown the need for correct adjustment of the hydrogen-ion concentration of the medium."

Various nutritional benefits have been suggested as accrueing to the host plant of an endophyte. It is supposed that nutrients are absorbed from the soil by the external hyphae of the endophyte, and translocated thence into the internal hyphae, which are eventually digested by the host cells. BURGES, however, agrees with the criticism that the connections between external and internal hyphae are insufficient for the host plant to benefit much in this way. TERNETZ (1904) demonstrated nitrogen fixation by certain species of *Phoma* acting as endophytes in members of the *Ericaceae;* the amounts of nitrogen so fixed were, however, too low to be of much nutritional significance to the host plants, and endophytes with a greater nitrogen-fixing capacity have yet to be discovered. BUTLER (1939) has made the interesting suggestion that endophytes of the vesicular-arbuscular type may benefit their host by the manufacture of accessory growth factors, which the host is unable to make for itself.

The relationship between the endophyte and its host seems to be one of controlled parasitism. Under certain conditions, the resistance of the host may be broken down, and the controlled parasitism become uncontrolled, as observed by REED and FRÉMONT (1935) and SAMUEL (1926). REED and FRÉMONT found that the roots of Californian citrus trees receiving no fertilisers during the preceding seven years had little power to resist invasion or to digest the intracellular mycelium, in contrast to the roots of trees which had been manured annually with cover crops and stable manure. SAMUEL observed that the roots of oats growing in a South Australian soil deficient in available manganese were heavily infected by an endophytic fungus, whereas the roots of oats growing in normal soils were free from infection. SAMUEL's observation recalls an analogous one by BRENCHLEY and THORNTON (1925), who found that root-nodule bacteria became destructively parasitic in the root tissues of broad bean plants deprived of boron. Again, a fungus forming a mycorrhiza with one host may act as a destructive parasite in others. An example of such behaviour is furnished by a dangerous parasite of forest trees and other plants, *Armillaria mellea,* which was demonstrated by KUSANO (1911) to form a mycorrhiza with the Japanese orchid *Gastrodia elata.* KUSANO observed, however, that under certain conditions the symbiosis might be upset, and that infection of the orchid tuber by *A. mellea* was then accompanied by a necrotic reaction of the invaded cells of the host.

From the evidence adduced above, BURGES has concluded that the

chief benefit which mycorrhizal plants derive from this association is that due to the decomposition of soil organic matter by the mycorrhizal fungi. Plants with ectophytic mycorrhizal fungi are, of course, exceptionally well situated for the reception of such benefit. As BURGES has pointed out, however, it is not necessarily the mycorrhizal fungi which are always of greatest service to the higher plant in this way; common soil-inhabiting fungi may conceivably be of greater importance to a mycorrhizal plant than its own particular fungal associate. The enhanced activity of certain common soil-inhabiting fungi, and especially of *Mucor* spp. and *Penicillium* spp., in the "rhizosphere" has been thought by JAHN (1934) to constitute a "peritrophic mycorrhiza." This interpretation of mycotrophy by BURGES has been criticised by HATCH (1937), in a masterly review of the subject to which he has himself made numerous important experimental contributions. HATCH has studied chiefly the ectophytic mycorrhizae of *Pinus,* and has interpreted his data by the "mineral salt hypothesis" of STAHL (1900).

Elsewhere, BURGES (1939) has commented upon the paucity of information concerning the saprophytic life of the mycorrhizal fungi. This would be the more surprising were it not for the fact that a similar obscurity surrounds the saprophytic life of a closely analogous but better known group of micro-organisms, the root nodule bacteria of leguminous plants. The mode of survival of mycorrhizal fungi outside their host plants therefore remains an unsolved problem, or series of problems, concerning which BURGES (1939) has commented: "This class of soil fungi is the most difficult of all to study. Many of its members appear to be almost obligate parasites in their relations to their hosts, yet their ubiquitousness leads one to believe that they must have some existence in the soil apart from their host roots. In isolation of soil fungi, it is rare to find any member of this group. Many are Basidiomycetes and these are conspicuous by their absence from lists of soil fungi. The typical ectotrophic mycorrhizas are produced by Hymenomycetes and many species have been identified." BUTLER (1939), in his review of work on the vesicular-arbuscular or phycomycetous type of endophyte, has observed that this endophyte is more common and more easily to be found in the roots of perennial or plantation crops than in the roots of annual field crops, *viz.:* "The regularity of its occurrence in some perennial plants and its incidental presence in some annual field crops is probably merely the result of the greater chance which an organism growing in close association with living roots has of persisting indefinitely and passing from the older to the more newly developed roots in the former class. In annuals, much of the fungus perishes with the roots, and survival is limited to the thick-walled resting mycelium and vesicles found in the soil when the new crop is sown."

*Chapter 3*

# PARASITIC ACTIVITY OF THE ROOT-INFECTING FUNGI

In the preceding chapter, a distinction was drawn between primitive parasites of the *soil inhabitant* type, such as the species of *Rosellinia,* in which parasitic activity was merely incidental to a saprophytic existence, and the more specialised parasites of the *soil invader* type. Variation in growth habit and parasitic activity of the latter group may now be considered.

The more specialised parasites spread underground in three ways:—

(1) through the soil and over the underground parts of the host plant,
(2) only over the underground parts of the host plant,
(3) inside the vascular system of the host plant.

Fungi belonging to the first two classes invade the internal tissues of the host roots, of course, but external spread never lags appreciably behind internal spread, and is often considerably in advance of it. The fungi of class (3) do not travel either independently through the soil, or over the outside of the host roots; their spread is limited to the vascular cylinder of the host. Spread of fungi in classes (2) and (3) from one host plant to another is therefore limited to points of root contact between host plants; this constitutes no hindrance to spread amongst crops where the ground is occupied by a pure stand of a susceptible host plant, except where the crop is still young, and root contacts have not yet been established. In natural vegetation, however, plants susceptible to a particular root parasite are often isolated from one another by the root barriers of immune plants, and so the spread of the parasite is restricted. At one time it was thought that a fungus able to spread independently through the soil by free mycelial or rhizomorphic growth possessed a considerable advantage over a fungus which could spread from host to host only by root contact; this distinction is now realised to have been over-drawn.

**Spread External to the Host:** — A feature of particular interest in the root-infecting fungi, though by no means limited to this group, is the rhizomorph—an organ whereby the fungus is enabled to spread from one host (or substrate) to another, some distance away. The evolution of the rhizomorph through aggregation of individual hyphae into strands, followed by differentiation of tissues into an external protective skin or rind, and internal conducting tissue, seems intrinsically probable; the rhizomorph serves to protect the mycelium of the fungus from the hazards of the environment, and especially from that of desiccation, and to facilitate its spread from one substrate (the food-base) to another, some distance away. The following fungi may be

cited as illustrating different, but not necessarily consecutive, hypothetical stages in evolution of the rhizomorph:—

(i) spread by individual hyphae—*Rhizoctonia solani* (causing black scurf and stem canker of potatoes, etc.).

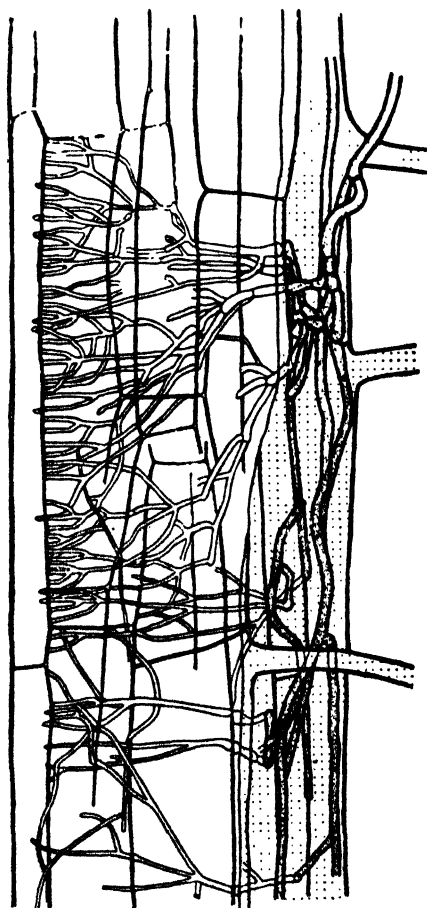



FIGURE 1*a*. — Runner hyphae of *Ophiobolus graminis* on seminal root of wheat. Longitudinal section. (*After G. Samuel*).

(ii) spread by individual hyphae occasionally aggregating into strands — *Ophiobolus graminis* (causing the take-all disease of cereals).

(iii) some aggregation of hyphae, with copious secretion of mucilage binding a covering of soil closely around host root—*Fomes noxius* (causing brown root disease of rubber, tea, etc.).

(iv) differentiated strands composed of large central hypha surrounded by several layers of fine hyphae — *Phymatotrichum omnivorum* (causing Texas root rot of cotton).

(v) aggregation into definite rhizomorphs, but no tissue differentiation — *Fomes lignosus* (white root disease of rubber, etc.).

(vi) aggregation into definite rhizomorphs with toughened outer skin — *Ganoderma pseudoferreum* (causing red root disease of rubber) and *Poria hypolateritia* (causing red root disease of tea).

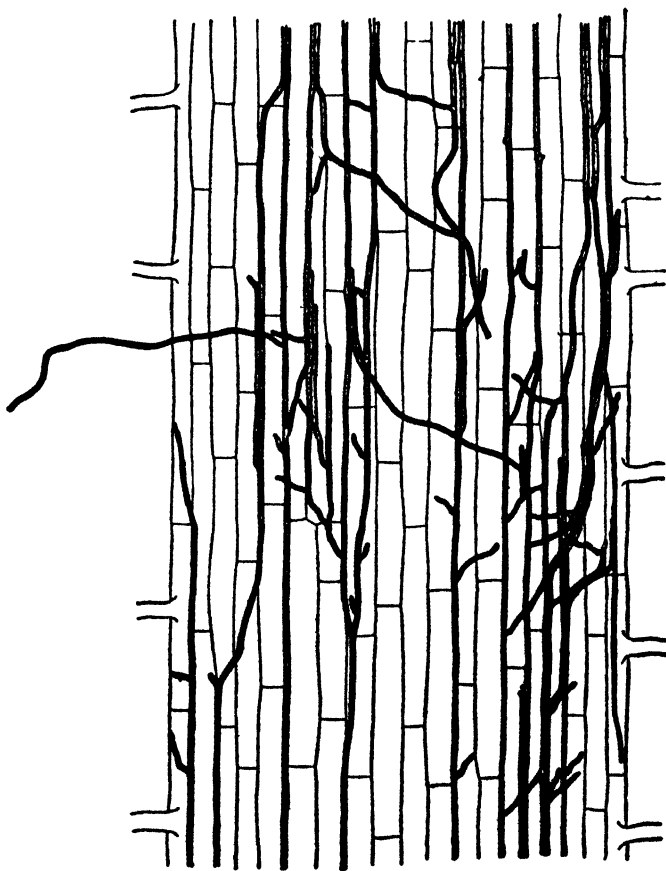



FIGURE 1*b*. — Runner hyphae of *Ophiobolus graminis* on seminal root of wheat. Surface view. (*After G. Samuel*).

(vii) aggregation into definite rhizomorphs with well differentiated outer rind — *Armillaria mellea* (causing a root disease of tea, cacao, etc.) and *Sphaerostilbe repens* (causing violet root rot of rubber, tea, citrus, etc.).

The mucilage-secreting power of *Fomes noxius* was discovered by SHARPLES (1922), who considered that the cementing of soil around the mycelium by this means provided a valuable safeguard for the fungus against desiccation. SHARPLES (1936) has laid great stress upon the function of the rhizomorph in protecting the fungus from

drying-out whilst external to the host tissues. The outer hyphal layers of the differentiated strands of *Phymatotrichum omnivorum,* the development of which has been described in detail by ROGERS and WATKINS (1938), no doubt help to protect the large central hypha from desiccation, though the strands do not seem to be particularly resistant to drying-out; even the sclerotia of *P. omnivorum,* unlike those of most other species, possess comparatively little resistance to desiccation (*see* below, p. 77). In *Armillaria mellea,* rhizomorphs are developed not only external to the host but also internally as well, between the bark and the wood; they were distinguished as *Rhizomorpha subterranea* and *R. subcorticalis,* respectively, by PERSOON (CAMPBELL, 1934). In *Sphaerostilbe repens,* rhizomorphs are formed only between the bark and the wood of the host root, though they show a degree of differentiation comparable to that in *Armillaria mellea.*

The capacity of a root-infecting fungus for making a free and independent spread through the soil from one host plant to another has frequently been a subject for controversy. Thus PETCH (1921, 1923) was convinced that both *Fomes lignosus* and *Poria hypolateritia* behaved in this way in the rubber and tea plantations of Ceylon. As a result of field observations on rubber estates in Malaya, NAPPER (1932-34) disputed PETCH's assertion that *F. lignosus* had more than a very limited capacity for free growth through the soil, and insisted that growth was almost entirely confined to solid surfaces; the fungus could travel over the surface of stones and dead wood buried in the soil, but could only infect and obtain nourishment from living roots.

In the U. S. A., TAUBENHAUS and KILLOUGH (1923) declared that *Phymatotrichum omnivorum,* the agent of cotton root rot, spread through the soil only along the roots of its host plants, and from one plant to another by root contact. This view was disputed by PELTIER *et al.* (1926), who asserted that *P. omnivorum* spread through the soil in the manner of a fairy ring fungus; their view, apparently, was based upon the observation that "the point of attack is nearly always on the tap root within the first foot of soil, whereas the lateral or side roots are usually diseased only at the point of attachment with the tap root. . . . If the spread of *Ozonium* occurred through the contact of a diseased root with a healthy one, then we should expect to find that the rot began at the ends of the laterals and worked up to the main tap root." Later, TAUBENHAUS and EZEKIEL (1930*a*) reported experiments designed to elucidate this question. Cubes of soil were taken from next to recently wilted plants in the active zones of root rot spots in cotton fields, and used to inoculate healthy cotton plants. Inoculations were made by removing soil from beside the healthy plant, watering heavily, and filling the hole with the soil inoculum from which all larger roots were first removed. Controls consisted of similar healthy plants which were inoculated with freshly infected cotton roots. Not

one of the 2367 plants inoculated with the presumably infective soil contracted the disease, whilst 180 of the 220 control plants, inoculated with infected roots, became infected. In another experiment, soil was again secured from the active zones of root rot spots in fields on three different types of soil; part of the soil of each type was passed through a ¼-inch sieve, and part was left unsifted, *i.e.* with all the original roots. Root rot appeared only in cotton planted in the unsifted soil

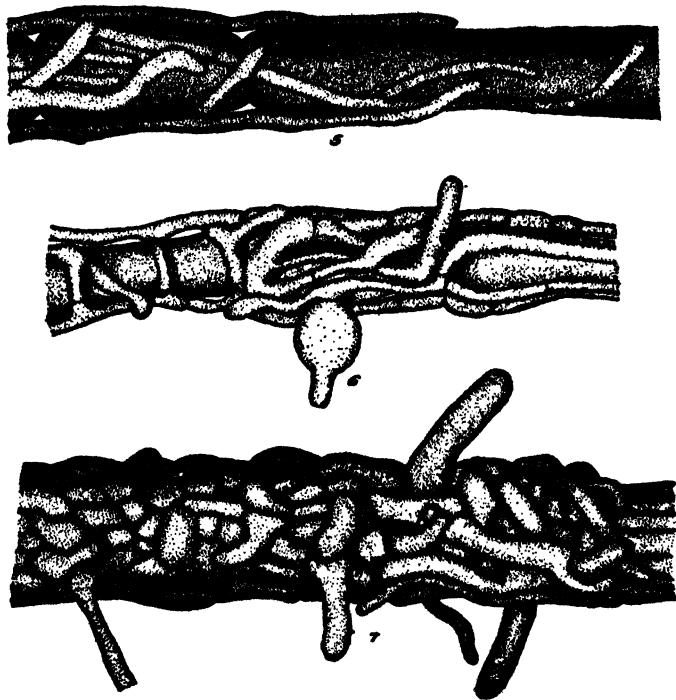



FIGURE 2. — Stages in mycelial strand formation by *Phymatotrichum omnivorum*. *5,* Small hyphae beginning to grow over the surface of a central hypha. *6,* Central hypha surrounded by a loose network of small hyphae. *7,* Deposition of the second hyphal layer. (*After C. H. Rogers and G. M. Watkins*).

containing the roots. Finally, TAUBENHAUS and EZEKIEL obtained further evidence by excavating the soil from about the roots of 117 cotton plants in early spring. Against selected plants, an isolation trench was dug, and the soil immediately around the root system was then carefully dissected away with stiff needles and with ice-picks. Each soil particle, as it was removed, was carefully examined under the hand lens for hyphae of *P. omnivorum,* and all roots and rootlets were similarly searched; doubtful material was studied under the microscope. No free spread of the mycelium away from the roots was discovered,

though the fungus was found travelling along the finest rootlets, and spreading from plant to plant by complete or proximate root contact. TAUBENHAUS and EZEKIEL pointed out that the finer infected rootlets might decay and disappear, leaving strands of the fungus apparently spreading freely through the soil; only close to the centres of well advanced spots were occasional isolated strands of the fungus found away from roots, and most of these were following insect or earth-worm channels through the soil. Nevertheless, when pieces of freshly infected cotton root were buried in natural unsterilised soil in glass

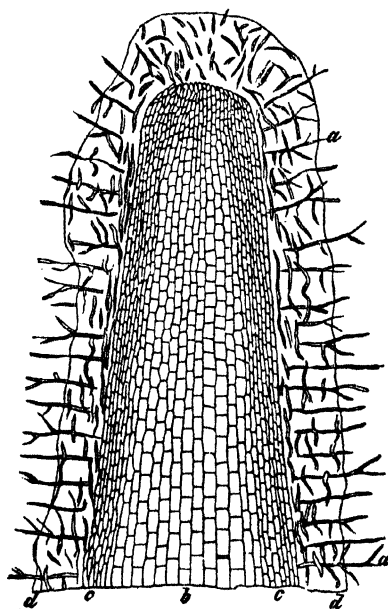



FIGURE 3. — Apex of rhizomorph of *Armillaria mellea* in longitudinal section. *a,* Mantle of filamentous hyphae. *b,* Central conducting cells. *c,* Cells of the rind. *d,* Boundary of enveloping mucilaginous layer. (*After R. Hartig*).

containers, mycelium of *P. omnivorum* grew from the roots out into the surrounding soil, the maximum observed extent of growth being 10 cm. away from the inoculum. The mycelium spread more readily along the wall of the glass container than through the soil itself, suggesting that *P. omnivorum,* like *Fomes lignosus,* kept to the continuous surface of a solid body where such was available.

Another well-known root parasite which has been shown to spread only by root contact is *Ophiobolus graminis,* cause of the take-all disease in cereals. PADWICK (1935) in Canada demonstrated through glasshouse experiments that whereas no appreciable spread of the fungus from buried inoculum occurred in fallow soil, a spread of as

much as 10 inches in 52 days took place under growing wheat and species of *Agropyron*. A very similar experiment was carried out in the field by ADAM and COLQUHOUN (1936) in South Australia; they compared the spread of *Ophiobolus* through a clay-loam soil and through sand, in which wheat seeds were planted at distances apart of 2, 4, 8 and 12 inches. At harvest, no detectable spread of the fungus had occurred where the plants were spaced 12 inches apart; a maxi-

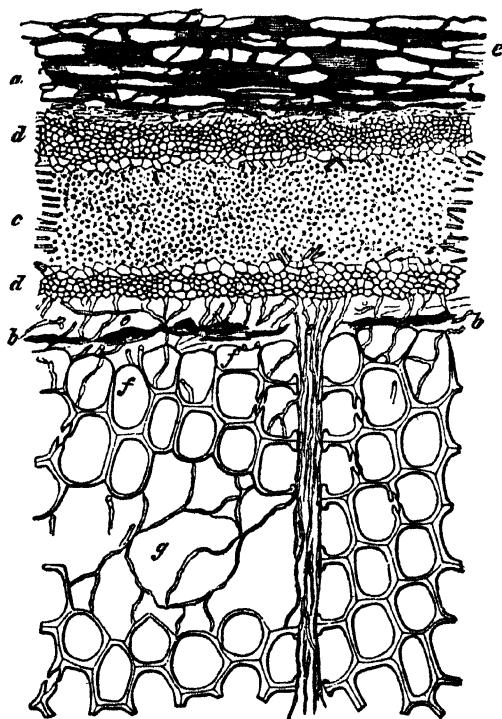



FIGURE 4. — Transverse section through cortex and wood of a pine root that has been invaded and killed by a rhizomorph of *Armillaria mellea*. *a*, Dead bast tissues. *b*, Dead cambium. *c*, Medulla of rhizomorph. *d*, Rind of rhizomorph. *e*, Individual hyphae that have grown out from the rhizomorph. *f*. Dead wood cells. *g*, Resin duct destroyed by the fungus. (*After R. Hartig*).

mum spread of 20 inches from the original inoculum was recorded under the plants spaced 2 inches apart. FELLOWS and FICKE (1939) in Kansas, have confirmed this conclusion as to spread of *O. graminis*. GARRETT (1936) was unable to demonstrate mycelial growth from inoculum of this fungus placed on the surface of unsterilised soil in covered glass dishes. Nevertheless, it has since been found that such growth will occur under special conditions, *e.g.* when freshly-infected straw is buried in moist sand against a glass surface; the mycelium of

the fungus then grows out over the glass, and may even form perithecia. Here, again, the fungus spreads over a continuous surface, but less readily, or not at all, over and through a discontinuous medium.

Root excavations carried out under tropical crops have led to a similar conclusion. Thus, concerning the spread of *Armillaria mellea* in tea and coffee plantations in East Africa, WALLACE (1935*a*) writes: "Hundreds of infected coffee and tea roots have been examined in Tanganyika and without exception infection has taken place from diseased roots lying against or in fairly close proximity to the dead bush. It is doubtful whether rhizomorphs have an effective range of more than a few feet, but this requires confirmation." A similar observation has been made by DADE (1927) concerning the same parasite on cacao in the Gold Coast; he states: "In each of the hundreds of cases which have been carefully examined infection has been found to be due to actual contact of the host's roots with other diseased roots or rotting wood." It must be added, however, that DADE found no rhizomorphs of *A. mellea* in the soil of these cacao plantations on the Gold Coast; he considered that the heavy texture of the soil may have inhibited their development. Concerning the spread of *Fomes lignosus* on rubber estates in Malaya, SHARPLES (1936) declares: "Hundreds of diseased trees have been carefully opened up, even to depths of four feet, and in every case, without a single exception, the diseased material, from which infection has spread, has been found in contact with the diseased roots at some point. . . . There has been such a large number of serious outbreaks which have been dealt with entirely successfully by simply keeping in mind that digging must be continued until the actual source of infective material has been discovered and extracted."

How, then, are we to reconcile such observations and experiments on the subterranean spread of root disease with earlier observations such as those of PETCH (1921)? The answer is simple enough; *it is essential to distinguish between spread of the fungus and spread of the disease.* Taking *Armillaria mellea* as an example, we may recall ELLIS' (1929) report that the rhizomorphs of this fungus had been found to extend for as much as 22 yards from an infected pit-prop in a mine working. Yet WALLACE (1935*a*) considered that the *effective* range of the rhizomorphs probably did not exceed a few feet. Further experimental evidence upon this point is obviously required.

*The food-base.*—The importance of the food-base behind the host-invading mycelium is coming more clearly to be recognised. Thus BLISS (1941) obtained infection with rhizomorphs of *A. mellea* only when these were attached to a suitable substrate; detached rhizomorphs were ineffective. From the first, the importance of organic connection between the infecting hyphae and the food-base behind them has been

generally admitted. Thus, concerning the spread of *Fomes lignosus* through the soil, PETCH (1921) observes: "It is always attached to its base, *i.e.* the stump on which it originated, and it must derive its food from that source until it meets with other dead wood, or a living plant which it can attack. In all probability it will die if separated from its base, unless it soon meets with fresh material from which it can derive nourishment." And some years later, concerning the difficulty of replacing the "natural" food-base with pure-culture inoculum of a root-infecting fungus, PETCH (1928) writes: "It is not possible to imitate these conditions from pure culture. If the fungus is grown in pure culture on agar, the amount of mycelium which can be used for inoculation is small, and the agar substratum usually soon disappears. If, on the other hand, the fungus is grown in pure culture on sterilised wood blocks, a similar difficulty is encountered. The volume of a block of wood which can be sterilised with certainty is small; about 1 cubic inch is usual. Moreover, although a vigorous growth of mycelium may occur, it will be found that this is chiefly external, and unless the cultures are allowed to develop for a long period, there will be little penetration of the wood block." TUNSTALL (1930) reported that he had successfully inoculated tea bushes with *Fomes noxius* by tying pieces of dead wood permeated by a pure culture of the fungus onto the roots, but not with any other form of inoculum.

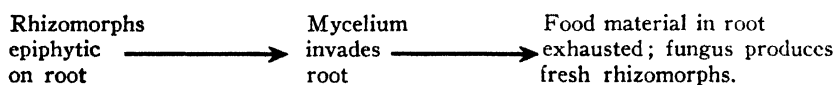
DE JONG (1933) has performed some illuminating inoculation experiments with *Fomes lignosus* on rubber trees. When pure cultures of the fungus on media other than wood, or the tissue of a fructification, were used as inocula, epiphytic growth of the fungus occurred on the surface of the root, but no decay, and the rhizomorphs eventually disappeared without having achieved infection. Successful infection was obtained only through the use of naturally or artificially infected pieces of wood for inoculation, and then only if the inoculum block was sufficiently large. Inoculation with pieces of wood carrying the fungus as an epiphyte failed to achieve infection more than occasionally, and even then the infection subsequently failed to progress. DE JONG noted that an infection might frequently be established and then fail to progress further; the decayed patches became surrounded by callus and eventually healed over completely. It was noticeable that the process of recovery usually started at about the time when the wood used for inoculation had itself disappeared through decay. Sometimes, however, the decay continued to progress after the exhaustion of the original inoculum, presumably owing to the weakening of the root by the infection. DE JONG's results are of particular significance, inasmuch as they underline the essential fact that infection is a "struggle" between the offensive forces of the fungus and the defensive forces of the root; the issue of the "struggle" is

likely to be decided by the extent of the reserves available on either side.

Similar results have been reported by other investigators. Thus BLISS (1941) reported failure to infect citrus roots with pure cultures of *Armillaria mellea* on nutrient agar or bran; he achieved success only with naturally or artificially infected wood. COOLEY (1942) was unable to infect apple roots with cultures of *Xylaria mali* on agar, or on small chips of infected wood, but secured success by the use of 2-inch lengths of infected twig. Similar difficulties were encountered by investigators working on *Phymatotrichum omnivorum*. Thus TAUBENHAUS *et al.* (1929), reporting on the use of freshly-infected roots as inoculum in experiments with *P. omnivorum*, remark: "Though the disease has been known for more than 30 years and investigated extensively, definite progress with it has been hindered by the nearly complete failure of experimental inoculations. Thus it was not until 1923 that the first experimental proof was furnished that *Phymatotrichum omnivorum* is the cause of root rot. KING (1923) inoculated cotton plants in the field by inserting cotton roots infected naturally or from artificial cultures, in a trench dug next to the roots of the plants, and then filling the trench with earth. TAUBENHAUS and KILLOUGH (1923) succeeded in inoculating cotton plants in sterilised soil with pure cultures on mulberry stems or cotton roots."

It seems probable, therefore, that infection of the host root by mycelium or rhizomorph will be favoured by proximity to the food-base, by efficient translocation of food material along the mycelial strands or rhizomorphs, and by ample reserves in the food-base; it will be hindered by both passive and active defences of the host, *i.e.* by thick cork barriers on the one hand, and by active wound reactions on the other. As GADD (1936*a*) has pointed out in a general discussion of this subject, fungi such as the species of *Rosellinia,* which can use leaf-mould and other decaying organic detritus on the surface of the soil as a food-base, possess an advantage in their resulting ability to make a rapid surface spread in favourable (*i.e.* moist and shady) situations; surface spread in such a situation is necessarily more rapid than underground spread. Experiments are certainly needed to determine the effective parasitic range of rhizomorphs from a food-base; the translocation of food material along the rhizomorphs of *Armillaria mellea* must be efficient enough to account for a spread of such distance over an inhospitable surface as that recorded by ELLIS (1922), cited above. Conduction must be remarkably efficient even along the undifferentiated rhizomorphs of *Fomes lignosus,* for NAPPER (1938*b*) states that they may be epiphytic on the rubber root for as great a distance as 15 feet ahead of actual penetration by the fungus; infection, of course, takes place immediately in advance of preceding infection, in a continuous wave.

The rhizomorph cycles in the three important root-infecting fungi found on rubber in Malaya are of much comparative interest; whereas the rhizomorphs of *F. lignosus* commonly extend for a distance of 5-15 feet epiphytically along the root in advance of penetration, those of *F. noxius* and *Ganoderma pseudoferreum* are usually found only some 18 inches in advance of the infected zone (NAPPER, 1938*b*). In consequence of this difference, the proportion of total infected trees to dead trees will be higher with *F. lignosus* than with the other two parasites. Considering any particular section of a rubber root about to be invaded by one of these fungi, the cycle of infection and rhizomorph production may be shown as follows:

Rhizomorphs epiphytic on root ⟶ Mycelium invades root ⟶ Food material in root exhausted; fungus produces fresh rhizomorphs.

Concerning this process, NAPPER (1934) writes: "In nature the process is more or less continuous. Infection progresses in a steady wave, the advancing column of rhizomorphs being the sum of the contributions from numerous successive cycles at small phase intervals.

"The production of rhizomorphs from infected tissue is probably a reaction to starvation conditions, the stimulus to production being brought into play when the fungus has completely gutted its host of all available food material and, although continuing to inhabit the empty skeleton, is forced to draw upon its own reserves for the necessities of life. Rhizomorphs are never produced from newly-infected tissue where there is ample food material available for the nourishment of the fungus. Note here the close analogy with fruit body formation."

In view of the nutritional requirements for root infection discussed above, it is not surprising that no investigator appears to have reported successful inoculation of any tree root with a spore suspension. LEACH (1939) failed to achieve infection either of tree roots or of the cut surfaces of stumps by inoculation with basidiospore suspensions of *Armillaria mellea.* An apparently similar limitation was found by GARRETT (1939*b*) to prevent infection of wheat roots by the ascospores of *Ophiobolus graminis* under natural soil conditions. In numerous experiments with natural soils, with steamed (*i.e.* partially sterilised) soils, and with sand, GARRETT was unable to secure any ascospore infection of the roots, either in seedlings or in older plants. The ascospores germinated well on agar, and the agar cultures thus obtained were able to infect wheat seedlings in a normal manner. Satisfactory infection by ascospores was finally obtained by using sterile wheat seedlings growing in sterilised soil or sand, to which was added a suspension of ascospores in sterile water. By reference to the work of BROWN (1922) on leaf infection by the spores of *Botrytis cinerea,* GARRETT concluded that the ascospores of *O. graminis*

required an external food supply before they could establish root infection. In sterile sand, such food material was assumed to be provided by the root excretions of the wheat seedlings, which would be wholly available to the germinating ascospores; in unsterilised sand, on the other hand, such root excretions would be quickly assimilated by other micro-organisms around the roots.

**Spread Internal to the Host:** — A different method of subterranean spread is found amongst the vascular parasites, such as *Verticillium albo-atrum* and the wilt-producing species of *Fusarium*.

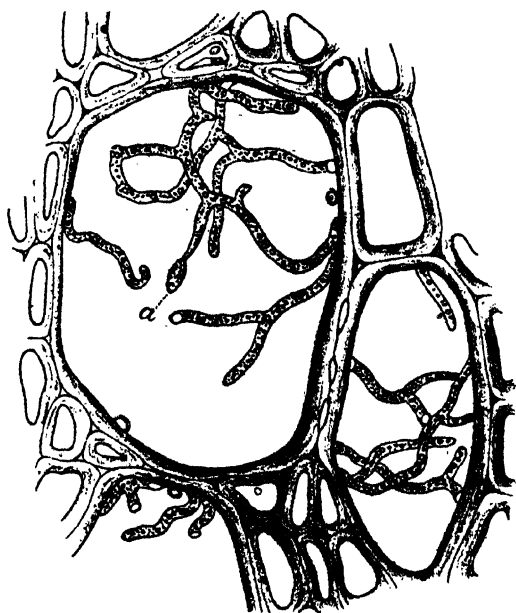



FIGURE 5. — Mycelium of *Verticillium albo-atrum* in water-conducting vessel of potato. (*After J. Reinke and G. Berthold*).

After passing through the cortex opposite the point of invasion, the fungus enters the water-conducting elements of the xylem (hence the name tracheomycoses applied to diseases caused by these fungi), along which it spreads in either direction. It does not leave the vascular cylinder until death of its host plant is imminent. No means of active spread through the soil except from plant to plant by root contact has been demonstrated for any fungus belonging to this group; quarantine measures based on this assumption appear to have been completely successful in limiting the *active* spread of Panama disease (*Fusarium oxysporum cubense*) of bananas in Jamaica (COUSINS and SUTHERLAND, 1930). From these observations, it follows that *a root does*

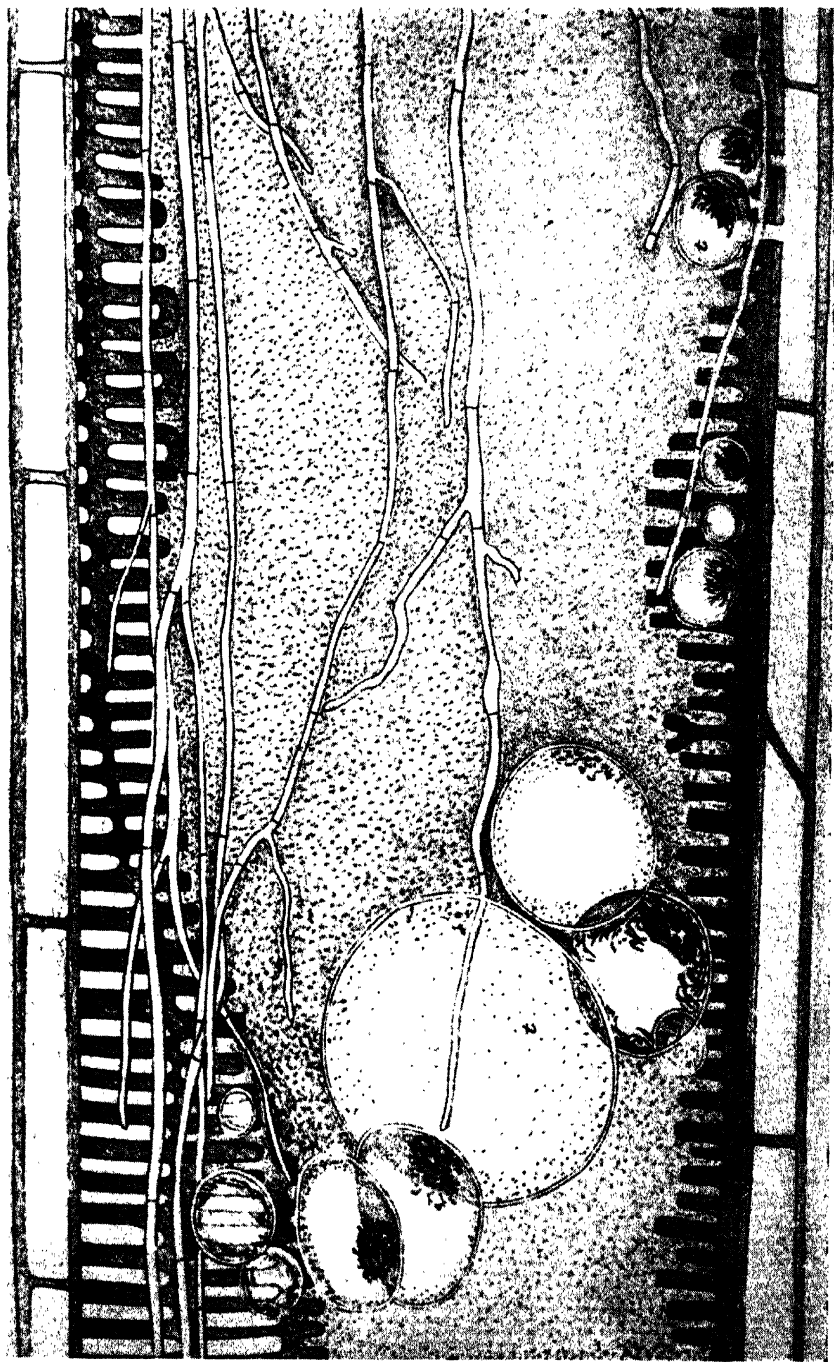



FIGURE 6. — Mycelium of *Fusarium oxysporum cubense* in water-conducting vessel of banana. *t*, Dead tyloses. (*After C. W. Wardlaw*

*not become infectious to other roots in contact with it as soon as it has become infected, because the fungus does not emerge from the vascular cylinder until the disease reaches its penultimate phase in the plant.*

In an experiment to test this assumption, ROBERTS (1943) found that approximately twice as many tomato plants became infected in a given time around *Verticillium*-infected plants that had died as a result of bark-ringing as became infected around similar *Verticillium*-infected plants that had not been ringed and still remained alive. Some data obtained by McKAY (1926) in field experiments on *Verticillium* wilt of potatoes may be interpreted by the same hypothesis. McKAY reported that the periodical rogueing of wilted plants throughout the growing season did not decrease the incidence of infection amongst immediately adjacent plants in the same row, but actually increased it, from 19 to 24.4% (the percentage infection was estimated at the end of the season by determining the proportion of infected tubers). Single-plant rogueing of infected individuals would not, of course, be expected to check the spread of the disease, but the slight though probably significant increase in spread was perhaps rather surprising. McKAY himself suggests the following explanation: "It seems reasonable to suppose that where diseased plants are rogued the roots of adjoining plants would grow more freely into the area formerly occupied by the diseased plant, and since in rogueing diseased plants many *Verticillium*-invaded roots would be broken off and left in the ground the chances of spread might be increased rather than decreased." On the basis of ROBERTS' experiment, McKAY's explanation may perhaps be supplemented by suggesting that the violent removal of wilted plants from the ground, in the act of rogueing, hastened the death of those portions of infected roots left behind in the soil, with the result that the fungus emerged from the vascular cylinder of such roots earlier than it would have done had the plants been left undisturbed.

*Chapter 4*

# INFLUENCE OF SOIL TEMPERATURE UPON PARASITIC ACTIVITY

Soil conditions may influence the occurrence of soil-borne disease in a variety of ways. Most important is their direct influence upon the parasitic activity of the root-infecting fungi, and their indirect influence through the medium of host resistance. Of less importance is their effect upon survival of the fungi during periods between susceptible crops. If the soil is favourable to the development of disease, the amount of infectious material left behind in the soil for infection of the next susceptible crop is much increased. It thus happens that soil conditions often influence the survival of a root-infecting fungus more strongly in an indirect way, *viz.* by increasing or by decreasing the amount of inoculum left in the soil, than in a direct way by their effect on the survival of a given quantity of inoculum. To take a specific example, TAUBENHAUS *et al.* (1937) showed that both incidence of cotton root rot in the current season, and the amount of *Phymatotrichum omnivorum* surviving in the soil to the next cotton season, were greater in alkaline than in neutral or acid soils; a greater bulk of the fungus survived the winter in such soils because the amount of inoculum left behind in the soil after cotton harvest was greater. It is quite possible, therefore, that survival of unit quantity of inoculum was greater in acid or neutral soils than in alkaline soils. Indeed, in experiments upon the take-all disease of wheat, GARRETT (1938*b*, 1940) and FELLOWS (1941) showed that survival of *Ophiobolus graminis* was greatest under those conditions of soil temperature, aeration and moisture content least favourable ( *i.e.* within the experimental ranges employed by them) to parasitic activity of the fungus.

Another way in which soil conditions may affect the incidence of disease is through their influence upon dispersal or passive spread of the parasite; fungi may be spread, for instance, through the agency of floods, or by irrigation.

In this and the two following chapters, the influence of soil conditions upon the incidence of soil-borne disease may now be examined and discussed under the following heads:—

| | | | |
|---|---|---|---|
| (i) | temperature | (iv) | reaction |
| (ii) | moisture content | (v) | organic content |
| (iii) | texture | (vi) | concentration of plant nutrients. |

For this purpose, free use will be made of a previous compilation by GARRETT (1938*a*). In analysing these observations and experimental results, the following generalisation may be kept in mind: ***soil conditions will exert the greatest direct influence upon those root-infecting fungi that spread chiefly by mycelium external to the host, and***

*the greatest indirect influence, through the physiology of the host, upon those fungi that spread only inside the host.*

**Temperature:** — Soil temperature exercises an important effect upon the occurrence of soil-borne diseases, often determining not only their relative prevalence at different times of the year, and from one year to another, but also their geographical distribution. Our knowledge of the operation of this factor is due very largely to the work of L. R. JONES and his collaborators at the University of Wisconsin, a monographic account of which has been given by JONES *et al.* (1926). The Wisconsin school developed the well known soil temperature tanks for the study of soil-borne diseases under controlled temperature conditions; they did not confine themselves to a study of the temperature factor alone, but concurrently investigated the effect of variation in soil moisture content and other component factors of the soil environment. The accurate control of soil temperature that they obtained was later followed by control of air temperature as well, though this refinement has not added much to the important results previously obtained by the use of the soil temperature tanks alone. Experiments carried out in the temperature tanks on development of a particular soil-borne disease were supplemented by a study of the growth of the parasite at different temperatures in pure culture; last but not least, extensive records of soil temperatures were collected in the field, for correlation with prevalence of soil-borne diseases at different times of the year, and from one year to another. The importance of such supplementary field observations is emphasized by JONES *et al.*, who remark: "The environment under which such plants are grown experimentally is never duplicated under natural conditions of growth. For example, the experimental soil temperatures here discussed were, as a rule, held approximately constant or else at two regularly alternating points as contrasted with the irregular fluctuations in nature. The avoidance of hasty and unsound judgments has been, therefore, best insured in our experience through coupling field studies with those of the greenhouse. Close observations as to disease development under natural conditions in the field correlated with field temperature records greatly increases one's confidence in the interpretation of such experimental data." Such a conjunction of extensive field data with the results of controlled temperature experiments in the Wisconsin tanks may be considered to have established certain important soil-borne diseases as high temperature diseases, and others as low temperature diseases; diseases favoured by high temperature are cabbage yellows (*Fusarium conglutinans*), tomato wilt (*F. bulbigenum* var. *lycopersici*), flax wilt (*F. lini*), and seedling blight of wheat (*Gibberella saubinetii*), whilst diseases favoured by low temperature are onion smut (*Urocystis cepulae*), tobacco root rot (*Thielaviopsis basicola*), stem canker of

potatoes (*Rhizoctonia solani*), and seedling blight of corn (*Gibberella saubinetii*).

The optimum temperature for development of cabbage yellows, a vascular wilt, in the Wisconsin tanks, was found by TISDALE (1923) to be approximately 26°C., whilst the optimum temperature for growth of *Fusarium conglutinans* on agar was the same. The temperature optima for development of two other vascular wilts were only a degree or two higher. The optimum for tomato wilt was found by EDGERTON and MORELAND (1920) to be 29°C., and by CLAYTON (1923*a*) to be 28°C., and the optimum temperature for growth of *Fusarium bulbigenum* var. *lycopersici* on agar was determined by CLAYTON as 28°C. The optimum for flax wilt was found by JONES and TISDALE (1922) to be 24°-28°C., with an optimum of 26°-28°C. for growth of *Fusarium lini* on agar.

An interesting contrast between the behaviour of the tomato wilt due to *Fusarium bulbigenum* var. *lycopersici* and that of another vascular wilt of tomato due to *Verticillium albo-atrum* was demonstrated by BEWLEY (1922) in England. BEWLEY found the optimum temperature for development of *Verticillium* wilt to be 21°-23°C.; at 25°C. and above, development of the disease was inhibited. He inoculated his plants by hypocotyl stab and and not through the soil; infection occurred at 25°C., but made comparatively little progress in the vascular cylinder, and seemed to have no adverse effect upon growth of the tomato plant. BEWLEY also found that wilted plants could be "cured" by transferring them to a glasshouse in which the average temperature was not less than 25°C.; if such plants were later moved back to the lower temperature house, the persistence of the "cure" appeared to vary directly as the duration of the high temperature treatment. The beneficial effect of high temperature in assisting recovery was found to be augmented by shading the plants. At the same time, BEWLEY gave data concerning the occurrence of these two vascular wilts of tomato in England, which supported both his own conclusions concerning *Verticillium* wilt and those of the American workers concerning *Fusarium* wilt. *Verticillium* wilt had been found to occur more frequently in England than *Fusarium* wilt, which was comparatively rare. *Verticillium* wilt normally appeared about the middle of April and increased in intensity up to the second or third week in May. The attacks usually died down during the second half of June, were scarce or absent altogether in July and August, and reappeared at the end of September, when the plants died prematurely. *Fusarium* wilt, on the other hand, occurred at the hottest part of the season, usually in July and August.

The optimum temperature for development of onion smut, a low temperature disease, was found by WALKER and JONES (1921) to be 19°-22°C.; the optimum temperature for germination of chlamydo-

spores and hyphal fragments was shown by WALKER and WELLMAN (1926) to lie between 15° and 20°C., a range which is lower than the optimum temperature for vegetative growth of the majority of fungi (25°C.). WALKER and JONES further discovered that the onion seedling was susceptible to infection by *U. cepulae* only via the young parts of the cotyledonary leaf, which later became covered by the sheathing bases of the outer leaves. The period during which infection of the young plant could occur from the soil was limited to about three weeks; higher soil temperatures were therefore thought perhaps to diminish the chances of infection by reducing the length of this susceptible period.

A similar effect of high soil temperatures in diminishing infection by hastening the emergence of sprouts was thought by RICHARDS (1921, 1923*a*) to play some part in reducing incidence of stem canker of potatoes due to *Rhizoctonia solani* at higher soil temperatures. Thus FREDERIKSEN *et al.* (1938) recently demonstrated in Denmark that deep planting (12 cm.) of tubers aggravated the incidence of stem canker, whereas shallow planting reduced it to a minimum. RICHARDS determined the optimum temperature for development of stem canker as 18°C.; above 24°C., little damage was caused by this parasite. The optimum temperature for growth of *R. solani* in pure culture is approximately 25°C., but stem canker damage was found to be worst at 18°C. not only in potato but also in cotton, pea and bean (RICHARDS, 1923*b*). In view of the fact that development of some of these hosts was better at temperatures above 20°C., and that of others was better below this temperature, RICHARDS concluded that the temperature optimum of 18°C. for stem cankering was connected in some way with the physiology of the parasite rather than with that of the host, nor was it to be wholly explained by the "disease escaping" result of more *rapid* growth (a high temperature may promote more rapid emergence of a plant from the soil, but the same plant may eventually make its greatest growth at a lower temperature). RICHARDS therefore suggested that, although 25°C. might be the optimum temperature for (most rapid) growth of *R. solani* on agar, a lower temperature might promote the best production of enzymes or toxins essential for development of parasitism. Some strains of this fungus are known, however, to have a much higher optimum temperature for disease production; LECLERG (1934) found the optimum temperature for development of root rot in sugar-beet to be 25°-33°C., and VASUDEVA and ASHRAF (1939) demonstrated that the root rot of cotton due to *R. solani* in India was most severe at 35°C.

Tobacco root rot, another low temperature disease, was found by JOHNSON and HARTMAN (1919) to develop best at 17°-23°C.; at 26°C. the damage was considerably reduced, and at 29°C. the amount of infection was negligible. The optimum temperature for growth

of *Thielaviopsis basicola* in pure culture, however, was found to be 28°-30°C. CONANT (1927) studied the reaction of varieties of tobacco, susceptible and resistant to *T. basicola,* to infection at temperatures of 20°, 25° and 30°C. He observed a close correlation between cork formation and resistance to infection, both in the resistant variety, which was resistant at all three temperatures, and in the susceptible variety, which was resistant at 30°C. JONES *et al.* (1926), commenting upon CONANT'S (then unpublished) results, remark: "The difference between susceptible and resistant plants may not be primarily in relative potential phellogen activity but in the fact that the resistant plant has some inherent quality or characteristic which so slows down the fungus invasion as to permit time for such cork formation to occur. In any case, however, the 'corking-out' of the fungus is the final and evident expression of the fungus-resisting reaction." This reservation made by JONES *et al.* in accepting CONANT'S conclusions in full has been confirmed by JEWETT (1938), who was unable to substantiate CONANT'S claim that resistance to *T. basicola* could be correlated with cork formation; she concluded that resistance was not associated with any such anatomical factor.

A comparison was made above between two vascular wilt parasites of the tomato, *Fusarium bulbigenum* var. *lycopersici* and *Verticillium albo-atrum,* with widely different temperature optima for disease production in the same host. DICKSON (1923), in a now classical study of seedling blight in wheat and corn, demonstrated that a single fungus, *Gibberella saubinetii,* might have widely different temperature optima for disease production in different hosts, *viz.* wheat and corn. Whereas seedling blight developed to the greatest extent in corn at low soil temperatures (8°-16°C.), the disease affected wheat seedlings most severely at relatively high soil temperatures (16°-28°C.). The optimum temperature for development of seedling blight in each cereal was therefore that furthest removed from the optimum temperature for development of the underground parts of the host plant. DICKSON, and DICKSON *et al.* (1923), further elucidated the reasons for this difference in temperature optimum for disease development, as follows. The cell membranes of the seedling sheath of both wheat and corn are at first composed chiefly of pectic substances, and are easily penetrated by *G. saubinetii;* under conditions optimum for plant development, the membranes pass quickly through the susceptible pectin stage to the mature condition, in which celluloses and even lignin or suberin predominate. These less easily hydrolysable cell wall constituents were found to resist penetration by the parasite. Under adverse conditions of temperature, *i.e.* in corn sown at low temperatures and in wheat sown at high temperatures, this natural development of resistance is retarded; other adverse conditions, such as too low a moisture content of the soil, or too low a light intensity, were found to

produce the same result. DICKSON and HOLBERT (1926) demonstrated a similar sequence of events in their study of resistance to seedling blight in susceptible and resistant lines of corn at a range of temperatures.

Results obtained in the investigation of two other soil-borne diseases of wheat show a curious discrepancy, upon which JONES *et al.* comment. The optimum temperature for development of the disease caused by *Helminthosporium sativum* in wheat seedlings was found by McKINNEY (1923) to be about 28°C.; the optimum temperature for development of the take-all disease, due to *Ophiobolus graminis,* was found by McKINNEY and DAVIS (1925) to lie between 12° and 16°C. The optimum temperature for growth of both fungi on agar was 25°C. McKINNEY and DAVIS pointed out that whereas the high temperature optimum for the disease caused by *H. sativum* was readily explicable as being most favourable for activity of the fungus and least favourable for development of the wheat plant, this expectation was contradicted by the behaviour of the take-all disease. This puzzling anomaly was brilliantly resolved by HENRY'S (1932) experiments on development of the take-all disease at different soil temperatures. In unsterilised soil, HENRY obtained a disease-temperature curve similar to that of McKINNEY and DAVIS for *O. graminis,* with a peak of 18°C.; in sterilised soil, however, the curve more nearly resembled that of McKINNEY for *H. sativum,* inasmuch as the temperature optimum had shifted upwards. HENRY therefore suggested that the fundamental disease-temperature curve for *O. graminis* had been obtained in sterilised soil, but that in unsterilised soil an uncontrolled factor, *viz.* microbiological antagonism to the parasite, had increased with rise of temperature and, by curtailing the activity of *O. graminis,* had masked the effect of rising temperature upon the host-parasite relationship. HENRY'S findings were confirmed by GARRETT (1934*a*), who found the optimum temperature for development of the disease to be approximately 24°C. In a review of published and unpublished work on the relation between cereal foot rot diseases and soil temperature, GARRETT (1934*b*) applied HENRY'S conclusions to other data, and showed that the masking effect of microbiological antagonism, which increased with rise in temperature, appeared to be more pronounced where cultures of the parasites on cooked cereal grains had been used as inoculum than where spore suspensions had been employed. In the ultimate analysis, therefore, the difference between the results of McKINNEY (1923) with *H. sativum* and those of McKINNEY and DAVIS (1925) with *O. graminis* might be attributed to the fact that *H. sativum* produces conidia profusely in culture (a spore suspension was used by McKINNEY as inoculum), whereas *O. graminis* is usually sterile (a mycelial culture on oat and barley kernels was therefore employed by McKINNEY and DAVIS as

inoculum). From a review of all available experimental evidence, GARRETT (1942) has concluded that the take-all disease is favoured by high soil temperatures, with an optimum around 25°C. A similar interaction of microbiological antagonism with temperature has been suggested by SCHROEDER and WALKER (1942) to explain their observation that whereas wilt disease of pea due to *Fusarium oxysporum* f. *pisi* race 1 developed in an unsterilised virgin soil most rapidly at 18°C., in sterilised sand with nutrient solution it developed most rapidly at 27°-30°C. As a postscript to the discussion of this particular problem, a quotation from JONES *et al.* must now be credited with prognostic significance: "A second difficulty constantly requiring consideration in such work is that of eliminating the occurrence of variables other than the one under consideration which was, of course, soil temperature in most of the cases here discussed."

Temperature optima may be widely different not only for the development of different parasites in the same host and for the development of the same parasite in different hosts, but even for different phases of infection by one parasite in a single host. For example, PORTER and MELHUS (1932) found that whereas pre-emergence rot of water-melon seedlings due to *Fusarium bulbigenum* var. *niveum* was more severe at a low temperature (16°-18°C.) than at a high temperature (25°-28°C.), the wilting of the young seedlings was more serious at the higher temperature. An almost identical observation has been made by GREEVES and MUSKETT (1936), who found that whereas pre-emergence killing of swede seedlings by *Pythium debaryanum* was greatest at the lowest temperature (6°C.) in their experiment, the damping-off of the emerged seedlings was greatest at the highest temperature (23°C.). Both pairs of investigators attributed the high incidence of pre-emergence killing at low temperatures to delayed emergence of the seedlings.

It follows, therefore, that temperature may determine not only the intensity but also the type of infection within the host plant. Thus SCHROEDER and WALKER (1942) have pointed out that two vascular wilt fungi, *Fusarium oxysporum* f. *pisi* race 1 and *F. niveum,* cause extensive cortical decay of the roots when the host plant is grown under adverse temperature conditions. Thus *F. oxysporum* f. *pisi* produces root necrosis in peas grown at too high a temperature (27°-30°C.), whereas *F. niveum* behaves similarly in water melons grown at too low a temperature (16°-18°C.).

Lastly may be considered the effect of soil temperature upon the occurrence of a soil-borne disease in the field; this may be expressed in at least three different ways, (i) by variation in incidence of the disease according to the time of year, whereby control can sometimes be secured in practice through alteration in date of planting, (ii) by fluctuation in prevalence of the disease from one year to another, (iii)

by limitation of the geographical distribution of the disease. No better examples of the last effect can be given than those quoted by JONES *et al.*: "It is strikingly exemplified in the case of onion smut. Wherever this occurs in the United States, it is an introduced parasite. The fungus spores are regularly transported with diseased bulbs and especially with onion sets from smutted fields, as well as in other ways with such soil. As a result, since first detected in Massachusetts about fifty years ago, it has insidiously spread and established itself across the northern States. Its complete absence in the Gulf States, where it has been regularly introduced with onion sets finds a surprisingly simple explanation when one knows how temperature, during the germination period, functions as a limiting or 'conditioning' factor. . . . The cabbage *Fusarium* (cabbage yellows disease) is quite regularly serious in the second tier of northern States from New Jersey to Iowa and occurs in the southern parts of the most northern States, *e.g.* New York, Wisconsin. It disappears, however, as one proceeds northwards in these northernmost States primarily, we believe, because the summer temperatures are not regularly quite warm enough."

*Chapter 5*

# INFLUENCE OF SOIL MOISTURE CONTENT, TEXTURE, AND REACTION UPON PARASITIC ACTIVITY

**Moisture Content:** — Diseases known to be favoured by high soil moisture content are given in Table 1, taken from GARRETT (1938*a*).

TABLE 1. *Diseases favoured by high soil moisture content:* —

| FUNGUS | DISEASE | AUTHORITIES |
|---|---|---|
| *Plasmodiophora brassicae* | Clubroot of crucifers | MONTEITH (1924), NAOUMOVA (1933) |
| *Spongospora subterranea* | Powdery scab of potato | BLATTNÝ (1935) |
| *Synchytrium endobioticum* | Potato wart | GLYNNE (1925), ESMARCH (1926) |
| *Aphanomyces euteiches* | Root rot of pea | F. R. JONES & DRECHSLER (1925), HAENSELER (1926) |
| *Pythium arrhenomanes* | Root rot of sugar-cane | FLOR (1930), CARPENTER (1934) |
| *P. arrhenomanes* | Root rot of corn | JOHANN *et al.* (1928) |
| *Sclerospora graminicola* | Seedling blight of Italian millet | TASUGI (1935) |
| *Phytophthora cactorum* | Crown rot of rhubarb | BEACH (1922) |
| *P. cambivora* | Ink disease of chestnut | BLIN (1922) |
| *P. cinnamomi* | Pineapple wilt | LEWCOCK (1935) |
| *P. parasitica* | Various | BEWLEY (1923), PETRI (1929) |
| *Fusarium annuum* | Chilli pepper wilt | CRAWFORD (1934) |
| *F. cubense* | Banana wilt (Panama disease) | WARDLAW (1935) |
| *F. lycopersici* | Tomato wilt | E. E. CLAYTON (1923), WHITE (1926) |
| *F. orthoceras* var. *pisi* | Pea wilt | STARR (1932) |
| *Fusarium* sp. | Celery yellows | RYKER (1935) |
| *Armillaria mellea* | Mushroom root rot | DADE (1927), GARD (1927) |
| *Calonectria graminicola* | Snow mould of cereals | ELENEFF (1926) |
| *Helminthosporium sativum* | Foot rot of cereals | MCKINNEY (1923) |
| *Sclerotinia sclerotiorum* | Collar rot of lettuce | SOURSAC (1922) |
| *Sphaerostilbe repens* | Violet root rot of tea | TUNSTALL (1922) |

The first eleven diseases listed in Table 1 are due to phycomycetous fungi and other organisms which infect the host by means of free-swimming zoospores; when soil moisture content falls below a certain value, infection is usually completely inhibited. Thus MONTEITH (1924) found in controlled soil moisture experiments that infection of cabbage seedlings by *Plasmodiophora brassicae* occurred at moisture

contents of 60% saturation and above, but not at those of 45% saturation or below; the severity of infection increased with rise in moisture content. Similarly, SMITH and WALKER (1941) found practically no infection by *Aphanomyces euteiches* at a soil moisture content of 45% saturation, whereas 72% infection occurred at a moisture content of 75% saturation. HICKMAN (1940) has recently demonstrated that the occurrence of red core root disease of strawberries, due to *Phytophthora fragariae*, depends upon high soil moisture content.

The next five diseases on the above list are vascular wilts due to species of *Fusarium;* to these may be added *Fusarium vasinfectum*, which was found by THARP and YOUNG (1939) to produce maximum disease at a moisture content of 80-90% saturation. PONTIS (1940) reported percentage of wilt in chillies due to the same fungus to be increased by frequency of irrigation in a field experiment; satisfactory control of this disease was secured by planting "on the ridge". Evidence is accumulating to show that infection by the vascular wilt fungi, including *Verticillium albo-atrum*, is favoured by the "soft" type of growth promoted by high soil moisture content and heavy nitrogenous manuring (organic or inorganic); the opposite conditions seem to reduce the incidence and severity of this disease not so much by reducing the original number of root infections as by restricting the active development of the vascular parasite within the plant. This has been demonstrated by CLAYTON (1923), FISHER (1935) and COOK (1937) in experiments on the effect of nitrogenous manures upon the susceptibility of tomato to infection by *Fusarium bulbigenum* var. *lycopersici*, whilst very similar results have recently been obtained by ROBERTS (1943), working with the same host but with another vascular parasite, *Verticillium albo-atrum.*

In some situations, high soil moisture content may increase the prevalence of a soil-borne disease in another way, *i.e.* by flood dispersal. This factor is said by WARDLAW (1935) greatly to have influenced the distribution of Panama disease of bananas. Very high soil moisture content may also, by reducing soil aeration, injure the roots of the host plant and thus afford ingress to such parasites as *Sphaerostilbe repens*, the cause of violet root rot in various tropical and sub-tropical crops. Factors predisposing sugar-cane to *Pythium arrhenomanes* root rot under the conditions of high water table and impeded drainage in the heavy clay soils of the Louisiana sugar belt have been investigated by RANDS and DOPP (1938). Hydrogen sulphide and salicylic aldehyde were selected as examples of substances accumulating in soils under semi-anaerobic conditions, and the effect of these two substances upon the predisposition of sugar-cane to *Pythium* root rot in nutrient sand culture was tested. Hydrogen sulphide was not found significantly to intensify the effects of the disease. On the other hand, salicylic aldehyde in concentrations of 20 to 40 p.p.m., which had little if any

influence on cane growth in the absence of the fungus and showed no effect on the growth of the fungus in culture, apparently so predisposed the roots to infection in the presence of the fungus as to result in a reduction in weight of the plants from 2 to 7 times as great as that caused by the fungus alone.

Next for consideration comes a group of diseases that do not require a high soil moisture content for development, but are yet more severe in wet seasons, and may be virtually absent in unusually dry ones; root rot (*Phymatotrichum omnivorum*) of cotton and take-all (*Ophiobolus graminis*) of cereals fall within this class. EZEKIEL (1938) reported that whereas the presence or absence of cotton root rot in different sections of Texas seemed to be determined by the coincidence of favourable neutral to slightly alkaline soils with mean normal temperatures above 60°F., its prevalence from year to year was apparently limited chiefly by the rainfall from the beginning of April to the end of July. Multiple correlation analyses of root rot losses in 10 selected counties of Texas, in which the soils were approximately equally favourable for development of this disease, showed that an increase of one inch of rainfall in April or May was associated with an increase of about 15% in root rot, one inch in June with an increase of about 20%, and one inch in July with an increase of some 30% in the disease. Variation in August rainfall did not seem to affect the incidence of root rot. The prevalence of the take-all disease of wheat in Saskatchewan over the 5-year period 1923-27 was correlated by RUSSELL (1930) with aggregate rainfall for June, July and the first half of August, whilst GARRETT (1934*a*), from a historical survey of the 34-year period 1900-33 in South Australia, was able to correlate abundance of the same disease with aggregate rainfall during the spring months of August, September and October. Commenting upon the distribution of take-all in the Murray Mallee district of the same State, GRIFFITHS (1933, 1940) declared that little damage was done by the disease in localities with an average rainfall of 10-12 inches, but that as the rainfall increased, so did the disease become more prevalent.

Turning now to those diseases favoured by low soil moisture content, listed in Table 2 (GARRETT, 1938*a*), we find the cereal smuts conspicuous as a group. As soil moisture content decreases, aeration improves, and this may account for the increased activity of the *Actinomyces* spp. (SANFORD, 1926) and of the cereal smut fungi (RABIEN, 1927). LING (1941) has demonstrated, however, that soil moisture content affects the development of the stripe smut fungus (*Urocytis occulta*) within the rye plant, in addition to any effect that it may have upon the incidence of initial infection. A sufficiently low soil moisture content must also favour infection of young cereal

TABLE 2. *Diseases favoured by low soil moisture content:* —

| FUNGUS | DISEASE | AUTHORITIES |
|---|---|---|
| *Actinomyces poolensis* | Pox of sweet potatoes | POOLE (1925*a*) |
| *A. scabies* | Potato scab | MILLARD (1923), SANFORD (1923) |
| *Sorosporium reilianum* | Head smut of sorghum | CHRISTENSEN (1926) |
| *Sphacelotheca sorghi* | Covered smut of sorghum | REED & FARIS (1924*a*) |
| *S. cruenta* | Loose smut of sorghum | REED & FARIS (1924*a*) |
| *Tilletia tritici* / *T. levis* | Bunt of wheat | GIBS (1924), RABIEN (1927) |
| *Urocystis tritici* | Flag smut of wheat | FARIS (1933) |
| *Ustilago avenae* | Loose smut of oats | REED & FARIS (1924*b*), JOHNSTON (1927) |
| *U. levis* | Covered smut of oats | REED & FARIS (1924*b*), JOHNSTON (1927) |
| *U. hordei* | Covered smut of barley | RUMP (1926) |
| *Fusarium hyperoxysporum* / *F. batatis* | Stem rot of sweet potatoes | POOLE (1924) |
| *Gibberella saubinetii* | Seedling blight of wheat and corn | DICKSON *et al.* (1923) |

seedlings by retarding emergence; JONES and SEIF-EL-NASR (1940) have shown that infection of wheat by *Tilletia levis* and *Urocystis tritici*, of barley by *U. hordei*, and of millet and broom corn by *Sphacelotheca sorghi* is favoured both by a relatively dry soil and by deep sowing. DICKSON *et al.* (1923) demonstrated that the greater development of seedling blight of wheat and corn due to *Gibberella saubinetii* in drier soils was due to a retarded development of the normal host resistance; MUSKETT (1937) has recently shown a similar relationship to exist between *Helminthosporium avenae* and the oat plant.

**Texture:** — Relatively few soil-borne diseases appear to be favoured by soils of heavy texture, as shown by Table 3 GARRETT, 1938*a*).

The eye-spot disease of cereals is not a disease of the roots, but

TABLE 3. *Diseases favoured by heavy soils:* —

| FUNGUS | DISEASE | AUTHORITIES |
|---|---|---|
| *Cercosporella herpotrichoides* | Eye-spot disease of cereals | OORT (1936) |
| *Calonectria graminicola* | Snow mould of cereals | KORFF (1924), LAUBE (1926) |
| *Sclerotinia graminearum* | Snow mould of cereals | KHOKHRYAKOFF (1935) |
| *Sphaerostilbe repens* | Violet root rot of tea | TUNSTALL (1922), PINCHING (1925) |

affects the stem just above soil level; the inoculum, however, may be partly soil-borne. Recent work by SPRAGUE (1937) indicates that heavy soils favour the disease insofar as they promote a higher relative humidity of the atmosphere around the stem bases of the plants just above soil level, owing to impeded drainage. The snow mould diseases of cereals are also favoured by high soil moisture content; drainage of water from the melting snow is slower on the heavier soils. The relation between the occurrence of violet root rot and high soil moisture content, due to impeded drainage in heavy soils, has been noted by numerous observers.

The majority of soil-borne diseases seem to be favoured by light-textured soils, as indicated by the list in Table 4 (GARRETT, 1938*a*).

TABLE 4. *Diseases favoured by light soils:* —

| FUNGUS | DISEASE | AUTHORITIES |
|---|---|---|
| *Actinomyces scabies* | Potato scab | MILLARD (1923) |
| *Botryodiplodia theobromae* | Internal root rot of tea | TUNSTALL (1922) |
| *Fomes annosus* | Red rot of pines | ANDERSON (1921), FALCK (1930) |
| *F. lucidus* | Root rot of coconut palms | BRYCE (1924) |
| *F. noxius* | Brown root rot of tea and rubber | TUNSTALL (1930), PEELEN (1930) |
| *Fusarium cubense* | Panama disease of bananas | REINKING (1935) |
| *F. lini* | Flax wilt | BOLLEY & MANNS (1932) |
| *F. hyperoxysporum* } *F. batatis* | Stem rot of sweet potatoes | POOLE (1924) |
| *F. orthoceras* var. *pisi* | Pea wilt | WALKER & SNYDER (1934) |
| *F. vasinfectum* | Cotton wilt | YOUNG (1928), ZAPROMETOFF (1929) |
| *Fusarium* sp. | Collar rot of peas | MOORE (1923) |
| *Ophiobolus graminis* | Take-all of wheat | GARRETT (1936) |
| *Sclerotinia sclerotiorum* | Collar rot of lettuce | SOURSAC (1922) |
| *S. trifoliorum* | Clover rot | PAPE (1931) |
| *Spongospora subterranea* | Powdery scab of potatoes | WILD (1929) |
| *Tilletia tritici* } *T. levis* | Bunt of wheat | GASSNER (1925) |

The root-infecting fungi, and indeed fungi in general, are strong aerobes, and their activity must therefore be favoured by soils of light texture, insofar as these are characterised by a good natural diffusion of the soil gases. Potato scab and take-all of cereals appear to be diseases particularly affected by soil aeration. GARRETT (1936) demonstrated a close correlation between those soil conditions favouring the occurrence of take-all in the field and those favouring most rapid growth of *Ophiobolus graminis* along the roots of the wheat plant, *viz.* light texture, loose condition and alkaline reaction; the

paramount importance of soil aeration was subsequently proved by direct experiment (GARRETT, 1937). REINKING (1935) was able to correlate numbers of *Fusarium oxysporum cubense* in the soil with incidence of Panama disease of bananas on soils of different type in Central America; numbers of the organism and severity of the disease both increased with increasing percentage of sand and decreasing percentage of clay in the soil. REINKING comments upon his results as follows: "Apparently in heavily infected soil root infections are so numerous that the plant is unable to ward off attack, as has been shown to be possible by WARDLAW (1930), and severe disease is produced. When the organism is not present in the soil in large numbers the infections are less, and undoubtedly the plant is capable of warding off attack to a certain degree resulting in less severe disease. The effect of the different soil types upon the possible production or non-production of resistance within the plant to attack by the parasite apparently is not of such great importance." REINKING did not discover any connection between *p*H value of the soil and prevalence of the disease; WARDLAW (1941), on the other hand, recently voiced the following general conclusions concerning the distribution of Panama disease with soil type: "Spread by contact takes place more rapidly in some soils than in others; the more open the texture, and the more acid the soil, the more rapid is the spread of disease. Alternatively, clay soils and slightly alkaline soils appear to possess more 'resistance' to the disease. . . . Recent years have also shown that clay soils, for many years considered 'resistant', have eventually shown an even more rapid spread—a phenomenon for which no adequate explanation has so far been forthcoming. . . . The collective experience, practical and scientific, in Central America is that hydrogen ion concentration is the master factor determining the severity of Panama disease, followed by texture."

It is dangerous to conclude too readily that because the activity of a root-infecting fungus is favoured by good soil aeration, the disease that it causes will be more severe on light-textured soils, or, vice versa, that greater prevalence of the disease on such soils is to be attributed to enhanced activity of the parasite. It is necessary to remember that light-textured soils are usually naturally poor in plant nutrients and often acid in reaction, whereas heavy-textured soils tend to be better supplied with plant nutrients, and are more often neutral or alkaline in reaction. This point is brought out by consideration of the distribution of cotton root rot on different types of soil in Texas and Arizona. The mode of spread of *Phymatotrichum omnivorum* closely resembles that of *Ophiobolus graminis*. Yet whereas take-all is favoured by soils of light texture, and by any other condition making for improved soil aeration, cotton root rot, according to FRAPS (1936), is more prevalent in Texas on heavy-textured alkaline soils

than on light-textured soils of neutral or acid reaction. The association of this disease, however, may not be with heavy texture, but rather with the alkaline reaction of these soils (TAUBENHAUS *et al.*, 1937), or with their high water-holding capacity (EZEKIEL, 1938). The importance of the last-named factor is suggested by STREETS (1937), in commenting upon the distribution of cotton root rot in Arizona: "In Arizona root rot is noticeably more prevalent in the finer textured soils along streams and river bottoms and in alluvial valleys than on the coarser soils of the mesas. Under irrigation, however, it thrives in the coarser soils when their moisture content is maintained by frequent applications of water. In fact, the superior aeration in the mesa soils favours the growth of the organism."

Two other instances in which association between prevalence of a disease and light soil texture cannot be attributed to effect of soil aeration upon the parasite are found in Table 4. Cotton wilt, due to *Fusarium vasinfectum,* is greatly aggravated by potash deficiency (YOUNG, 1938), which is notoriously more common on light than on heavy soils. Internal root rot of tea, formerly attributed to *Botryodiplodia theobromae,* was shown by GADD (1928, 1929*b*) in Ceylon to be associated with lack of starch reserves in the root, due to excessive plucking and pruning; he further demonstrated that this condition actually *preceded* infection by *B. theobromae.*

These instances show, therefore, the need for caution in interpreting field observations on the association between soil texture, or any other soil character, and prevalence of a soil-borne disease.

**Reaction:** — Diseases favoured by acid soils are given in Table 5 and others favoured by alkaline soils in Table 6 (GARRETT, 1938*a*).

Here, again, the need for caution in interpreting such observations is apparent; field observations may be misleading owing to the common association between soil acidity, lightness of texture, and poverty in plant nutrients. Conclusions are more trustworthy for diseases of great economic importance; field observations on such diseases have usually been supplemented by experiments. Such experiments are more easily performed with diseases of annual or field crops than with diseases of plantation crops; for this reason, evidence available for correlating incidence of disease with soil conditions is both more abundant and more reliable for field crops than for plantation crops.

Prominent amongst the diseases favoured by acid soils are the vascular wilts caused by various species of *Fusarium,* to which, according to WARDLAW (1941), may be added banana wilt, better known as Panama disease. The better development of tomato wilt in acid soils, experimentally demonstrated by SHERWOOD (1923) and SCOTT (1926), has been confirmed by PHILLIPS (1940) and HARRISON (1940). It is perhaps remarkable that so few experiments seem to

TABLE 5. *Diseases favoured by acid soils:* —

| FUNGUS | DISEASE | AUTHORITIES |
|---|---|---|
| *Armillaria mellea* | Mushroom root rot | GARD (1928), REITSMA (1932) |
| *Botryodiplodia theobromae* | Internal root rot of tea | TUNSTALL (1929) |
| *Fomes annosus* | Red rot of pines | ANDERSON (1921), FALCK (1930) |
| *Fusarium conglutinans* var. *callistephi* and var. *majus* | Wilt of china asters | WAGER (1932), VOGLINO (1932) |
| *Fusarium oxysporum* var. *nicotianae* | Tobacco wilt | JOHNSON (1921) |
| *F. lycopersici* | Tomato wilt | SHERWOOD (1923), SCOTT (1926) |
| *F. vasinfectum* | Cotton wilt | TAUBENHAUS *et al.* (1928) |
| *Plasmodiophora brassicae* | Clubroot of crucifers | WELLMAN (1930) |
| *Spongospora subterranea* | Powdery scab of potatoes | JANCHEN (1921), BLATTNÝ (1935) |
| *Synchytrium endobioticum* | Potato wart | NĚMEC (1935) |
| *Ustilago hordei* | Covered smut of barley | FARIS (1924) |
| *Ustulina zonata* | Charcoal root rot | TUNSTALL (1922) |
| *Aphanomyces levis*, *Phoma betae*, *Pythium debaryanum* | Root rot of sugar-beet | ARRHENIUS (1924) |

TABLE 6. *Diseases favoured by alkaline soils:* —

| FUNGUS | DISEASE | AUTHORITIES |
|---|---|---|
| *Actinomyces poolensis* | Pox of sweet potatoes | POOLE (1925*b*) |
| *A. scabies* | Potato scab | MILLARD (1923) |
| *Calonectria graminicola* | Snow mould of cereals | SCHAFFNIT & MEYER-HERMANN (1930) |
| *Fusarium orthoceras* var. *pisi* | Pea wilt | STARR (1932) |
| *Monilochaetes infuscans* | Scurf of sweet potatoes | POOLE (1925*b*) |
| *Ophiobolus graminis* | Take-all of wheat | GARRETT (1936) |
| *Phymatotrichum omnivorum* | Cotton root rot | TAUBENHAUS *et al.* (1928), EZEKIEL *et al.* (1930) |
| *Thielavia basicola* | Black root rot of tobacco | MORGAN & ANDERSON (1927), DORAN (1931) |
| *Urocystis tritici* | Flag smut of wheat | FORSTER & VASEY (1929) |
| *Verticillium albo-atrum* | Tomato, etc., wilt | HAENSELER (1928), MARTIN (1931) |

have been undertaken to analyse the action of so clear-cut a factor as soil reaction upon the incidence of disease. The preference of club-

root of crucifers for acid soils, and of potato scab, take-all of cereals, root rot of cotton and black root rot of tobacco for alkaline soils is widely known, and has been repeatedly confirmed by experiment.

The greater prevalence of the take-all disease on alkaline soils was correlated by GARRETT (1936) with a more rapid growth of *Ophiobolus graminis* along the roots in such soils; he suggested that rate of growth of the fungus along the roots in soils of heavy texture and in acid soils was checked by the accumulation of respiratory carbon dioxide, and that alkaline soils increased fungal growth rate by acting as acceptors of carbon dioxide. By forced aeration, GARRETT (1937) secured as rapid a growth of this fungus along the roots in acid (*p*H 5.2) as in alkaline (*p*H 8.0) soils. Evidence in support of GARRETT'S hypothesis has been published by BLAIR (1943), working with *Rhizoctonia solani,* the mycelium of which grows freely through the soil. BLAIR found that whereas the growth of this fungus along Rossi-Cholodny slides was normally most rapid in soils of neutral reaction, yet when 1% of ground wheat straw or dried grass had been added to the soil growth was most rapid at a reaction of *p*H 8. In this instance, the respiratory carbon dioxide was provided not by the root and its rhizosphere, but by the micro-organisms decomposing the fresh organic material. In another experiment, BLAIR was able to eliminate the depressing effect of ground wheat straw upon growth of *R. solani* through the soil by keeping the soil container, open at top and bottom, in a closed vessel containing dishes filled with saturated solutions of strong alkali, which must rapidly have absorbed the carbon dioxide given off by the respiring micro-organisms decomposing the wheat straw.

An interesting sequel has followed the report of FORSTER and VASEY (1929) that flag smut of wheat was encouraged by application of lime in field plot experiments in Victoria. MILLIKAN (1939) was able to show in sand culture experiments that a deficiency of calcium markedly reduced the development of the disease; if the degree of deficiency was sufficiently great, the disease was completely inhibited. On the other hand, the addition of excess calcium to the nutrient solution significantly increased the incidence of infection. From the results of chemical analyses made on the plants at the end of their growth period, MILLIKAN postulated an optimum concentration of calcium in the plant for the development of this disease. These pot experiments, which were carried out in three consecutive years, were supplemented by field experiments at 4 different centres in Victoria during 1933-38. A variety of manurial and mineral treatments were tested in these experiments; wide variation in the mineral composition of the plants was induced by the treatments, as revealed by chemical analyses carried out 6 and 9 weeks after germination (considered by MILLIKAN to be the critical period for the development of

flag smut, in view of the fact that sori consistently appeared in these field experiments at some 11 weeks after germination of the wheat). As in the pot culture experiments, the only correlation between incidence of disease and mineral composition that could be established was that with lime content of the tissues. MILLIKAN again concluded that the evidence indicated an optimum content of calcium in the plant for the establishment of infection, and that any treatment which shifted the calcium content of the plant further away from this optimal value would result in a decrease of the disease. This optimum concentration of calcium was not the same in all the experiments, but appeared to change with variation in other soil factors. In none of MILLIKAN's field experiments did he repeat the results of FORSTER and VASEY (1929) by securing increased development of flag smut after liming; a simple explanation of this apparent anomaly, however, is suggested. The *p*H value of the soil in the untreated plots at Werribee, where FORSTER and VASEY made their observations, was 5.5; frequent applications of lime had changed the *p*H value to a maximum of 8.3 on those plots showing the highest percentage of flag smut. The majority of MILLIKAN's experiments, on the other hand, were carried out at Rutherglen, with soil reaction of *p*H 7.7, and at Walpeup, with soil reaction of *p*H 8.6. MILLIKAN remarks: "The most severe flag smut damage occurs in the Mallee district of Victoria, in which Walpeup is situated, where the soil contains a high percentage of limestone."

It is worth noting at this point an experiment carried out by LING (1941) on the development of stripe smut (*Urocystis occulta*) in rye plants grown in nutrient sand cultures. LING employed a three-salt nutrient solution comprising potassium di-hydrogen phosphate, calcium nitrate, and magnesium sulphate; the incidence of infection was lowest in the series receiving maximum potassium phosphate, and highest in that receiving equimolecular proportions of calcium nitrate and magnesium sulphate, but minimum phosphate.

The two diseases of wheat cited above, take-all and flag smut, which may both be encouraged by liming the soil, afford an interesting contrast; in the take-all disease, with activity of the fungus partly external to the host, soil reaction seems directly to affect the parasite, whereas in the flag smut disease, with development of the fungus almost wholly internal, soil reaction seems to operate upon the fungus through the physiology of its host plant.

*Chapter 6*

# INFLUENCE OF SOIL ORGANIC CONTENT AND CONCENTRATION OF PLANT NUTRIENTS UPON PARASITIC ACTIVITY

**Organic Content:** — Diseases reported to be encouraged by the application of organic material to the soil are given in Table 7, taken from GARRETT (1938*a*).

TABLE 7. *Diseases favoured by application of organic matter:* —

| FUNGUS | DISEASE | AUTHORITIES |
|---|---|---|
| *Tilletia tritici* } *T. levis* } | Bunt of wheat | RABIEN (1927) |
| *Urocystis tritici* | Flag smut of wheat | FORSTER & VASEY (1929) |
| *Ustilago zeae* | Corn smut | BORZINI (1935) |
| *Verticillium albo-atrum* | Tomato wilt | BEWLEY (1922), BRITTLEBANK (1924) |
| *Rosellinia arcuata* | Root rot of tea | TUNSTALL (1922), PETCH (1923) |
| *R. bunodes* | Root rot of tea | TUNSTALL (1922), PETCH (1923) |

The species of *Rosellinia* are well known saprophytes on leaf mould and other organic detritus lying in and on the soil; such organic material provides these fungi with a substrate not only for subsistence but also for spread, and at the same time with a food-base from which their attack on such plants as they may chance to encounter can most expeditiously develop. Nevertheless, the parasitism of these fungi is not confined to this type of environment; WATERSTON (1941) has described comparatively their parasitic activity in the two contrasting situations in which they cause patches of disease in tropical plantation crops, stating: "The areas affected with *Rosellinia* vary between two environmental extremes. The first consists of regions of unrestricted spread, where conditions of high rainfall and lack of sunshine due to intense shade encourage humus formation. Under these conditions, the fungus attack is in the nature of an advancing sheet. The fungus in this phase may not only derive its food saprophytically from decaying leaf mould but appears to behave as a dangerous though incidental parasite to the stems and roots of trees and shrubs encountered during the course of its advance. These conditions exist in some of the wetter areas as in Dominica where root diseases caused by *Rosellinia* spp. may act as limiting factors to lime production. In cases like these, the conditions which best suit the host plant, best suit the fungus also, with the result recorded by FAWCETT (1915), NOWELL (1916)

and Stell (1929) that the finest trees are most liable to attack and are most frequently killed.

"The second region which may be recognised is one of slow and restricted spread, found where rainfall is lighter, with little accumulation of humus or surface litter and where shade trees may be absent (South, 1913, Stockdale, 1908, and Briton-Jones, 1934). Under these conditions, the spread of the fungus is confined to root contacts or from fragments of wood or root stumps of susceptible hosts which have been aptly described by Gadd (1936) as 'food-bases'."

The higher incidence of infection by some cereal smuts in soils well supplied with organc matter seems to be due to a direct effect of the organic material on spore germination. Thus Rabien (1927) found that spore germination of the *Tilletia* spp. and incidence of bunt in wheat were both favoured by a high humus content of the soil. Noble (1924) reported that spore germination in *Urocystis tritici* was stimulated by the roots of non-susceptible plants (peas, beans, and rye), and by traces of certain volatile substances, such as benzaldehyde, salicylaldehyde, butyric acid, and acetone. Platz *et al.* (1927) found that crushed plant tissue encouraged the germination of spores of *Ustilago zeae* in closed chambers, and that this stimulating effect was due to the carbon dioxide given off; an atmospheric concentration of 15% carbon dioxide was found optimum for spore germination.

The action of organic matter in encouraging the parasitic activity of *Verticillium albo-atrum* seems likely to be an indirect one, operating through the physiology of the host plant; Roberts (1943) has found that the percentage of established infections in tomato increases with the amount of nitrogen supplied to the plant by the soil.

Soil-borne diseases observed to be checked by application of fresh organic material to the soil are listed in Table 8 (Garrett, 1938*a*).

Table 8. *Diseases controlled by application of organic matter:* —

| Fungus | Disease | Authorities |
|---|---|---|
| *Actinomyces scabies* | Potato scab | Sanford (1926), Millard & Taylor (1927) |
| *Fusarium lini* | Flax wilt | Bolley & Manns (1932) |
| *F. vasinfectum* | Pigeon-pea wilt | McRae & Shaw (1933) |
| *Ophiobolus graminis* | Take-all of wheat | Fellows (1929) |
| *Phymatotrichum omnivorum* | Cotton root rot | King *et al.* (1934*a*) |

Much attention has been paid of recent years to the possibilities of "biological control" of soil-borne diseases by application of fresh organic material to the soil. It is assumed that increased activity of the

saprophytes developing on the fresh organic material must occur at the expense of, and to the detriment of, the plant parasites. The assimilation, respiration and excretion of the saprophytes must compete with those of the parasites; metabolic products which are toxic to other micro-organisms may be produced by some saprophytes, and, in addition, the development of a high population of micro-organisms may encourage the parasitism of certain micro-organisms upon others. Historical reviews of the subject of microbiological antagonism and biological control have been published by FAWCETT (1931), GARRETT (1934*b*, 1939), WAKSMAN (1937, 1941), PORTER and CARTER (1938), WEINDLING (1938), and GARRARD and LOCHHEAD (1938); discussion here will be confined to the three most important of the diseases listed in Table 8.

Control of potato scab by green manuring with grass cuttings was first reported by MILLARD (1921). SANFORD (1926) suggested that such control was brought about through the antagonism to *A. scabies* of saprophytic species of bacteria developing on the decomposing green manure (rye grass). Further experiments by MILLARD and TAYLOR (1927) showed that the development of scab on potatoes grown in sterilised soil inoculated with *A. scabies* could be reduced by simultaneous inoculation of the soil with *A. praecox*, an obligate saprophyte of more vigorous vegetative growth than *A. scabies*. By increasing the proportion of *A. praecox* to *A. scabies* in the inoculum, the degree of scabbing on the test potatoes was reduced from 100% to nil. The sterilised soil evidently provided sufficient food material for a good development of *A. praecox*, and only a rather small increase of control was given by the admixture of grass cuttings, sterilised along with the soil. MILLARD and TAYLOR concluded that, whilst their tests were concerned only with the biological control of *A. scabies* by *A. praecox*, soil bacteria might exercise a similar controlling effect, as suggested by SANFORD. Experiments by GOSS (1937) convincingly demonstrated the controlling effect of the general soil microflora upon the development of scab, though he failed to secure any result with an inoculation of *A. praecox* alone.

Field control of the take-all disease of wheat in Kansas by the application of such organic materials as chicken and horse manure, green alfalfa, boiled oats and barley kernels, and potato flour was very briefly reported by FELLOWS (1929). GARRETT (1936, 1937, 1938*b*, 1940) has attempted to analyse this controlling effect of organic materials upon the take-all disease; as a result of his study of the spread of *Ophiobolus graminis* along wheat roots under different soil conditions, he suggested that addition of organic material to the soil would depress the parasitic activity of *O. graminis* insofar as it increased the concentration of carbon dioxide in the micro-atmosphere around the roots. He obtained striking reductions in the survival

period of *O. graminis* in infected wheat straw by incorporating fresh organic material, low in nitrogen content, with the soil (*see* Chapter 7). Working on the same disease, STUMBO *et al.* (1942) and CLARK (1942) have recently emphasised the beneficial manurial effect of such organic supplements in increasing the resistance to attack of the wheat plant.

The efficacy of organic manure for the control of root rot in irrigated cotton under continuous cultivation in Arizona has been established by KING *et al.* (1934*a*). These authors supported their hypothesis of microbiological antagonism as the mechanism of control by an extensive study of the soil microflora in the treated and control plots by the Rossi-Cholodny slide technique (EATON and KING, 1934), and by soil respiration determinations. They were able to demonstrate in this way that whereas the development of saprophytic organisms was most profuse in the slides buried in the manured plots, the mycelium of *Phymatotrichum omnivorum* was most abundant on the slides in the unmanured plots.

Further light has been thrown upon this controlling effect of organic amendments by the laboratory experiments of MITCHELL *et al.* (1941). Quart jars of clay soil, untreated and with additions of 1% superphosphate, 3% farmyard manure, and 3% chopped sorghum, respectively, were incubated at "optimum" moisture content for periods of 0, 5, 10, 15, 20 and 30 days, and then inoculated with agar blocks taken from a culture of *P. omnivorum,* or with infected roots. Mycelium of *P. omnivorum* quickly developed over the soil surfaces in jars filled with untreated soil or with soil + superphosphate; the mycelium showed little apparent disintegration during the 16-day observation period. In the soils receiving fresh organic material, however, mycelial growth either failed to occur, or else was followed by disintegration. In the soil + sorghum, growth of *P. omnivorum* was inhibited for the full 30 days after addition of the organic material to the soil; in the soil + farmyard manure, growth of *P. omnivorum* from the inoculum block occurred in those series that had been incubated for 20 days or more following the original addition of the organic material. Ability of *P. omnivorum* to grow out from the inoculum seemed to be inversely correlated with bacterial numbers in the different soil series. As a further indication of the susceptibility of *P. omnivorum* to the competition of other micro-organisms, MITCHELL *et al.* reported that the fungus failed to grow upon nonsterile cotton roots in culture flasks, even when the roots were quite fresh; growth was also inhibited if sterile cotton roots were inoculated with a pinch of field soil. The addition of 3% organic material to the soil also resulted in the rapid disappearance of a high proportion of *P. omnivorum* sclerotia; MITCHELL *et al.* demonstrated that whilst this effect was due in part to attack and decomposition of the sclerotia

by other soil micro-organisms, it was chiefly brought about by spontaneous germination of the sclerotia, under the stimulus of the organic amendments (*see* below, p. 79). In further experiments along the same lines reported by CLARK (1942), the antibiotic effect of the organic materials upon the viability of the sclerotia was more important than the direct stimulus given by such materials to sclerotial germination.

According to REA (1939), experiments on the use of organic manures for the control of cotton root rot under dry-land farming conditions in the Blackland region of Texas have not so far given encouraging results; the success of KING and his collaborators in Arizona may be attributed in part to the fact that their experiments were carried out on irrigated cotton, and in part to the special methods of manure placement and timing that KING (1937) has recommended (*see* below, p. 97).

**Concentration of Plant Nutrients:** — Generous application of artificial fertilisers is undoubtedly an effective way of reducing the proportion of crop lost through the agency of certain root diseases. According to GARRETT (1942), the proportional loss occasioned by the take-all disease of wheat is greatly aggravated by poverty of the soil in one or more of the three major plant nutrients. The common association between serious outbreaks of this disease and phosphate deficiency of the soil is well known from accounts by investigators in Australia, where the soils are apt to be very deficient in this nutrient. A generous supply of plant nutrients probably increases plant resistance chiefly by promoting a more rapid production of new crown roots to replace those destroyed by the disease, though an additional direct effect upon the resistance to infection of individual crown roots cannot be precluded (GARRETT, 1941).

Since the appearance of this review by GARRETT, STUMBO *et al.* (1942) have demonstrated that development of the take-all disease in potted wheat plants grown in a naturally infected Kansas soil might be frustrated by adequate applications of nitrogenous and phosphatic artificial fertilisers. They attributed the control of take-all obtained by FELLOWS (1929) with certain organic materials largely to the plant nutrients, especially nitrates, set free in the soil by decomposition of these materials; such control was experimentally demonstrated by CLARK (1942), whose results revealed a correlation between nitrate nitrogen set free in the soil through decomposition of the organic material, and the degree of disease control obtained. Especially striking was CLARK's demonstration of the effect of volume of soil per plant upon resistance of wheat to take-all; plants grown in 1 kg. of an infected Kansas soil suffered severely from the disease, whereas others grown in 9 kg. of the same soil escaped serious injury. A

paradoxical situation, which serves further to emphasise the paramount effect of plant nutrients upon the development of take-all in potted plants, has been reported from Australia by ANGELL (1943). A second crop of wheat grown in drums of soil inoculated with *O. graminis* in the previous season was perfectly healthy, whereas that grown in the non-inoculated drums (which served as controls in the previous season) was badly affected by take-all. This reversal of results in the second season was attributed on the one hand to depletion of nutrients under the heavy crop grown in the non-inoculated drums in the first season, and, on the other, to their conservation under the diseased crop grown in the inoculated drums.

Conservation of plant nutrients under patches of severely diseased plants in an annual field crop may be partly responsible for the failure of a disease to reappear in severe form on the same areas in the following season's crop. This phenomenon of disappearance of a disease from old areas and appearance in new ones under continuous cropping is well established, and has been described in connection with root rot of cotton by TAUBENHAUS and KILLOUGH (1923), MCNAMARA *et al.* (1931) and by many others, and in connection with take-all of cereals by GLYNNE (1935) and by FELLOWS and FICKE (1939). Discussing this problem, GARRETT (1938*a*) favoured the explanation put forward by TAUBENHAUS and KILLOUGH, that the chances of survival of a root-infecting fungus from one season to the next were reduced by the early death of infected host plants; a disease was therefore less likely to reappear on sites occupied by severely infected and early killed plants in the previous season than on sites occupied by apparently healthy plants infected relatively late in the season. Such a reduction of over-wintering inoculum under sites of severe disease patches must be held partly responsible for failure of the patches to reappear on the same sites in the following season's crop; at the same time, conservation of plant nutrients under the scanty crop in such patches must tend to increase plant resistance to the take-all disease, and also, under some circumstances (*see* next paragraph), to cotton root rot.

*Nitrogen.*—Nitrogenous fertilisers were found by JORDAN *et al.* (1939) to reduce losses due to root rot (*Phymatotrichum omnivorum*) in almost-continuous cotton sequences in Texas, whereas phosphatic fertilisers increased mortality. These opposing effects of nitrogen and phosphate upon incidence of root rot were most pronounced on the Wilson very fine sandy loam soil, and were less striking on the heavier soils of the Wilson series; they were smallest and least consistent on the Houston clays. From their analyses of root bark of plants taken from the same field experiments, ADAMS *et al.* (1939) obtained a highly significant negative correlation between nitrogen content and root rot mortality, and a highly significant positive correlation between phosphoric acid content and mortality. An inverse correlation, also

highly significant, was found between phosphoric acid and nitrogen contents of root bark samples. These results have been confirmed by BLANK (1941), who found nitrogenous fertilisers to reduce root rot mortality; phosphatic fertilisers had no significant effect upon incidence of root rot on Houston clay soils of Washington County (Texas), but on the less calcareous soils of Burleson County they significantly increased both incidence of disease and crop yield.

Reduction in losses from pea root rot, due to *Aphanomyces euteiches,* following application of nitrogenous fertilisers, has been reported by HAENSELER (1931) and by WALKER and MUSBACH (1939) from the U. S. A., and by GEACH (1936) from Australia. This effect of nitrogenous fertilisers was attributed by GEACH to direct action upon *A. euteiches,* which he found to be especially sensitive to the nitrogen content of the medium when growing on agar plates. Thus on cornmeal agar with 2% peptone, formation of oogonia and antheridia by the fungus was suppressed, and the mycelium alone was no longer culturable after 33 days at laboratory temperature. On cornmeal agar without peptone, however, oospores were formed, and these remained viable during the whole test period (60 days). Nevertheless, further evidence seemed to be needed to bridge the rather wide gap between the observed behaviour of *A. euteiches* in pure culture on the agar plate, and the reaction of the disease to the application of nitrogenous fertilisers to the soil. A more likely explanation has been suggested by SMITH and WALKER (1941), as a result of their experiments on the effect of nutrients upon development of the disease in continuous-flow nutrient sand culture; the incidence of disease, which was severe at the $1/10$ concentration of the basal solution, decreased as the nutrient concentration increased, so that only a low percentage infection occurred at the $3 \times$ concentration, and none at the $4 \times$ concentration of the basal solution. The amount of disease varied inversely as the total salt concentration of the solution, irrespective of its composition; contrary to results of fertiliser trials in the field, the nitrogen-containing salts were no more effective in disease control than were those containing potash and phosphate. SMITH and WALKER therefore suggested that the greater effectiveness of nitrogenous compounds in disease control in field trials was due to the fact, established by WHITE and ROSS (1939), that they increased the salt concentration of the soil solution much more than did corresponding quantities of the potassium and phosphorus salts used in commercial fertilisers. These results of SMITH and WALKER suggest, therefore, that no directly toxic effect of nitrogenous compounds, as such, upon *A. euteiches* is involved, as believed by GEACH. SMITH and WALKER further demonstrated that, once infection had occurred, its development could not be inhibited by changing the concentration of the basal nutrient solution from a low to a high level. In experi-

ments on agar, *A. euteiches* was found to show little reduction in linear growth rate even at 5 × concentration of the basal solution, but growth of the mycelium on agar can scarcely be considered a satisfactory criterion of the behaviour of the zoospores in a solution without agar. SMITH and WALKER have also incidentally pointed out that GEACH's observations on the poor growth of *A. euteiches* on pea-decoction agar with the addition of various nitrogenous compounds are most simply explained by reference to the high concentrations which he employed. Since the publication of these experiments by SMITH and WALKER, SCHROEDER and WALKER (1942) reported that the development of pea wilt due to *Fusarium oxysporum* f. *pisi* race 1 in nutrient sand culture was similarly checked by increase in concentration of the nutrient solution, when peas were grown at the favourable temperature of 21°C. On the other hand, at a temperature of 27°C., which is unfavourable to normal development of peas, disease development was greatest at the highest concentration of the nutrient solution.

Another disease that can be much reduced by application of nitrogen is root rot of sugar-beet due to *Sclerotium rolfsii.* In field experiments carried out in California, LEACH and DAVEY (1942) found that, on an average of all trials, 50 lbs. of nitrogen per acre reduced infection by some 28%, 100 lbs. by 54%, and 200 lbs. by 65%. Ammonium sulphate, anhydrous ammonia, calcium nitrate and cyanamide proved equally effective at equivalent nitrogen levels. LEACH and DAVEY found no evidence for a directly toxic effect of the nitrogenous compounds upon the parasite, since calcium nitrate gave as effective a control as did equivalent-nitrogen amounts of anhydrous ammonia; the former was non-toxic to the mycelium and sclerotia of *S. rolfsii.* The effect of nitrogenous fertilisers in reducing the disease was nearly as pronounced in fields of high fertility as in fields of low fertility, which suggested that increased resistance of the sugar-beet was associated with a luxury consumption of nitrogen rather than with the correction of a deficiency, in the usual sense of this term.

Deficiency of nitrogen, on the other hand, has been claimed by CLAYTON (1923) and FISHER (1935) to inhibit infection of tomato by the vascular wilt fungus, *Fusarium bulbigenum* var. *lycopersici.* COOK (1937), however, concluded from his experiments that nitrogen deficiency did not inhibit infection by the fungus, but did check its development in the plant. The position has been further clarified by ROBERTS (1943), working with another vascular parasite of tomato, *Verticillium albo-atrum.* ROBERTS found that the number of infected plants increased with the amount of nitrogen supplied to the soil; in some experiments, infection in some of the nitrogen-deficient plants was confined to the root system or even to a single root, suggesting that nitrogen deficiency may act as much, or more, by hindering or in-

hibiting development of the fungus in the vascular tissues as by preventing initial infection of the root from the soil. It is pertinent to note here that a bacterial vascular parasite, *Phytomonas stewarti,* was found by SPENCER and MCNEW (1938) to cause most severe wilting in maize plants that had received excess nitrogen; under conditions of nitrogen deficiency, little or no wilting occurred.

The damping-off of pine seedlings was found by HARTLEY (1921) to increase directly with the nitrogen content of the soil. WRIGHT (1941) has correlated damping-off (due chiefly to *Rhizoctonia solani* and *Pythium ultimum*) amongst seedlings of deciduous trees with nitrate nitrogen content of the soil; he reported that the stand of seedlings was increased almost three-fold by the application of dextrose to the soil, whereby the nitrate nitrogen content was temporarily reduced.

*Phosphate.*—Browning root rot of cereals due to *Pythium arrhenomanes* and other *Pythium* spp. in Canada was reported by VANTERPOOL (1930-40) to be associated with a low phosphate and high nitrate status of the soil; VANTERPOOL has stressed the analogy between behaviour of this disease and that of sugar-cane root rot, studied by CARPENTER (1934), which is also caused, apparently, by *Pythium arrhenomanes* (DRECHSLER, 1936). The cereal disease can be controlled by application of a soluble phosphate, which does not seem to reduce the proportion of roots infected by the fungus, but, by greatly increasing the total number of roots produced, increases the number of functional roots. The disease was stated by VANTERPOOL to be worse in crops after fallow than in those sown on stubble land, in contrast to experience with other cereal root rots. This was attributed by VANTERPOOL to increase in the available nitrogen content of the soil after fallowing, as a result of nitrification. A possibly analogous case has been reported by GRANDFIELD *et al.* (1935), who found in Kansas that stands of alfalfa seedlings were progressively decreased through damping-off by *Pythium* spp. with increase in the preceding period of fallow from two to five years. Thus only 33% of the original stand of alfalfa seedlings survived till the following spring on the five years fallow plot, as compared with a survival of 70% on a plot under rotation of sorghum, corn, wheat, oats and alfalfa.

Wilt disease (due to *Fusarium vasinfectum*) of pigeon pea, on the other hand, was reported by MCRAE and SHAW (1933) to be aggravated by applications of superphosphate on the manurial plots at Pusa, although the crop gave a positive response in yield to this fertiliser (*cf.* the results of JORDAN *et al.* (1939) and BLANK (1941) with *Phymatotrichum omnivorum,* discussed above).

*Potash.*—The effect of potash in reducing incidence of cotton wilt, due to *Fusarium vasinfectum,* has been studied by YOUNG (1938), in a nine years' series of field experiments carried out at 15 different

centres in Arkansas. Field observations at an earlier date had indicated a correlation between incidence of "rust", correctly attributed by ATKINSON (1892) to potash hunger, and that of the *Fusarium* wilt. YOUNG found that fertilisers containing potash gave control of rust and at the same time reduced wilt in every year and at every location, except two. Increasing applications of potash gave, up to a point, increased control of the wilt. Whilst nitrate alone had little or no effect on the incidence of wilt, the application of acid phosphate and nitrate together appeared to aggravate both rust and wilt; where acid phosphate was used alone, the effect was still more pronounced. YOUNG'S results have been confirmed in Alabama by DICK and TISDALE (1938) in a factorial experiment involving all possible combinations of N, P and K at three different levels; joint applications of nitrogen and potash were found to reduce incidence of wilt, whereas phosphate increased it, and substantially reduced the beneficial effect of applying potash. SMITH (1940), announcing the results of two seasons' cooperative manurial trials in 13 localities of 9 States of the U. S. A., confirmed this beneficial effect of potash in reducing cotton wilt. In Uzbekistan, ZAPROMETOFF (1929) found the incidence of wilt to be very slight on soils with a high content of common salt, which suggests that salt might be able to replace potash for control of wilt and rust in cotton, just as it can be used to replace potash for the manuring of sugar-beet.

A reduction in the percentage of tubers infected by the potato wart organism, *Synchytrium endobioticum,* has been claimed by LESZCZENKO and SZYMÁNSKI (1938) to follow application of potash salts to artificially inoculated field plots in Poland. In experiments on the relation between development of clubroot in crucifers and the concentration of plant nutrients, PRYOR (1940) found the percentage of plants forming clubs to be markedly reduced by a deficiency of potash.

*Minor elements.*—Secondary infection by fungi and other microorganisms may complicate and aggravate the symptoms of minor element deficiencies in plants. Thus GERRETSEN (1937) has claimed that bacterial infection of the roots is concerned in the production of the "grey leaf" symptoms characteristic of manganese deficiency in oats. In Victoria, MILLIKAN (1938) found that applications of zinc sulphate at rates of 15 and 30 lbs. per acre considerably improved the growth of wheat crops suffering from a combined attack of eelworm (*Heterodera schachtii*) and of a number of root-rotting fungi, including *Helminthosporium sativum, Curvularia ramosa, Fusarium culmorum,* and *Rhizoctonia solani.* The treatment did not apparently give any appreciable reduction in the number of roots infected by the parasites, but, by greatly increasing the rooting capacity of the plant, minimised the damage due to such infection. MILLIKAN (1942) has

since demonstrated that soil micro-organisms may compete with a wheat crop for available supplies of minor elements. A deficiency of available zinc was made good by steam sterilisation of the soil; in steamed soils, wheat no longer responded to application of this minor element. The responsiveness to zinc could be restored, however, by re-inoculation of the soil with unsterilised soil two months before sowing wheat. From the results of such experiments, MILLIKAN concluded that the poor growth of wheat on certain Victorian soils was due more to competition by saprophytic soil micro-organisms for limited supplies of zinc and other minor elements than to root infection by parasites.

*Chapter 7*

# SAPROPHYTIC ACTIVITY OF THE ROOT-INFECTING FUNGI

The parasitic activity of the root-infecting fungi has been closely studied by many investigators; their saprophytic existence under natural conditions in the soil has received comparatively little attention, though the earlier literature abounds in assertions as to the capacity of this or that fungus for indefinite survival as a saprophyte in the soil; such statements have usually been deemed self-evident, though sometimes they have been supported by reference to the capacity of the fungus for maintained saprophytic growth on sterile culture media or in sterilised soil. With the realisation of the part played by competition of organisms in the microbiology of the soil, such assertions have become appreciably more rare, but the need for experimental investigation is still very great.

Two types of saprophytism can be distinguished amongst the root-infecting fungi: —

(i) active saprophytic colonisation of dead plant tissues lying on or in the soil,
(ii) limited saprophytic survival in tissues originally invaded as parasite.

The first type of behaviour is typical of the primitive parasites of the *soil inhabitant* class, and the second of the more specialised parasites of the *soil invader* class.

**Active Saprophytism:** — Root-infecting fungi behaving as active saprophytes will be considered, for convenience, under the following three heads: —

(i) Fungi making a macroscopically-visible saprophytic spread through the soil,
(ii) Fungi making a microscopically-visible saprophytic spread through the soil,
(iii) Fungi making no extensive saprophytic spread through the soil.

*Fungi making macroscopically-visible saprophytic spread through the soil.*—The species of *Rosellinia* may be selected as furnishing the best known examples of this class. These fungi are especially important in West Indian plantations; their biology and control has been described in detail by Nowell (1923), from whose book the following general description is taken: "In the West Indies the fungi concerned are mainly species of *Rosellinia.* Other forms occur but are comparatively rare. In cultivations of an open nature where sun and wind have access to the soil, and specially in those of arable crops, there is a rapid dissipation of the decaying material necessary for the development of the fungus and the diseases as a rule soon disappear.

They can persist, however, in cultivations such as that of cacao in which the conditions, especially where shade trees are abundant, approach to those of the forest in respect of shade and humidity. They also occur in windbreaks and hedges of certain susceptible trees and shrubs in wet or sheltered districts. The causative fungi infect shaded soil rich in decaying vegetable matter and spread slowly through it, destroying every plant with which they come into contact." A description of a particular occurrence of *Rosellinia arcuata* in Ceylon, which reveals the observer as well as the observed, has been contributed by PETCH (1928): "Almost my first experience of *Rosellinia arcuata* was its occurrence in a Panax hedge round my bungalow garden at Peradeniya. A mango tree which stood on the adjoining estate had been felled and the log left lying with one end near the hedge. The *Rosellinia* began to develop among the dead leaves which had accumulated alongside the log, and then spread to the hedge, where it ran along the surface of the ground under and among the dead leaves in the hedge bottom. As the mycelium reached each of the closely-planted Panax stems, it enveloped it at the base. The cortex of the Panax stem rapidly became soft and rotten, and in a very short time the plant was dead. In a few weeks the hedge had been killed for a length of about 6 feet. It was then considered that sufficient information had been obtained concerning the method of progress of the fungus."

*Fungi making microscopically-visible saprophytic spread through the soil.*—Free mycelial spread of *Rhizoctonia solani* through the soil can easily be demonstrated under the dissecting microscope; it is necessary only to place an agar inoculum disc of this fungus on the surface of moist unsterilised soil in a covered dish, and examine again in a few days' time. BLAIR (1943) has studied the spread of this fungus through the soil, using the Rossi-Cholodny slide technique. Growth of the fungus in 4 types of soil was most rapid at the lowest soil moisture content tested, 30% saturation, and was improved by forced aeration of the soil. Growth was depressed by addition to the soil of such fresh organic material as ground wheat straw or dried grass. BLAIR showed that this depression was due chiefly to the competitive effect of other micro-organisms better able to develop upon such substrates; under sterile conditions, the organic supplements failed to depress the growth of *R. solani*. Pre-decomposed materials depressed the growth of the fungus less than the fresh materials. In pure culture experiments on cellulose substrates, BLAIR demonstrated that the cellulose decomposing capacity of *R. solani* was weak by comparison with that of typical strong cellulose decomposers. He further analysed this depressing effect of the cellulose decomposing microflora upon the growth of *R. solani* by demonstrating that (i) the effect was much diminished by addition of excess nitrogen to the soil, and was there-

fore due in part to competition for available nitrogen between the cellulose decomposers and *R. solani* (ii) the effect was also greatly reduced by removal of the respiratory carbon dioxide produced by the cellulose decomposers, through absorption over strong alkali in closed vessels. In other experiments, BLAIR demonstrated that whereas growth of *R. solani* through untreated soils was most rapid at *p*H 7, in soils with fresh organic amendments the optimum *p*H value for growth was approximately 8; this he attributed to the action of alkaline soil as a carbon dioxide acceptor (GARRETT, 1936).

Although such experiments with Rossi-Cholodny slides demonstrated an effect of soil conditions upon the rate of growth of *R. solani* through the soil, they offered no clue as to how far such growth was supported by the 6-mm. disc of agar inoculum, and how far by nourishment from the soil itself. In an attempt to answer this question, BLAIR carried out experiments on the growth of the fungus through glass tubes filled with three different types of moist soil and with quartz sand, respectively; the tubes were inoculated at one end with an agar inoculum disc of the same diameter. Whereas growth of the fungus ceased at a distance of some 5 cm. from the inoculum in the tubes of sand, it extended for some 20 cm. beyond the inoculum in the three types of soil, during 21 days. In another experiment, BLAIR removed the agar inoculum disc from some tubes 2 days after the start of the experiment, and inoculated other tubes not with agar discs but with mycelial strands picked off the vertical glass walls of petri dishes containing agar cultures of the fungus. Removal of the agar inoculum discs after 2 days, or the substitution of mycelial strands as inoculum, greatly diminished the growth of *R. solani* in the tubes of sand; in the three soils, however, removal of the agar discs reduced growth by only a negligible amount. Growth of the fungus from the mycelial strand inoculum had almost caught up with that in the undisturbed agar disc controls after 23 days in one type of soil, but in the other two soils growth was only about half that in the agar disc control tubes after 23 days. BLAIR suggested that a certain *food-potential* of the inoculum might be necessary to initiate saprophytic growth of *R. solani* through the soil—by analogy with the need of most root-infecting fungi for a *food-base* before they can establish root infection (*see* above, p. 26).

The saprophytic persistence of *R. solani* in the soil has been correlated by ELMER (1942) in Kansas with summer weather conditions. ELMER states: "The commercial potato crop in eastern Kansas matures and usually is harvested in early June. Throughout the rest of the summer the fields usually remain fallow. Summer temperature in this area is too high for the production of *Rhizoctonia* sclerotia as is disclosed by the fact that they are rarely found here on tubers of the early summer crop. Thereafter the fungus must consequently exist

saprophytically as soil-borne mycelium. In this state its persistence depends on the presence of sufficient soil moisture to prevent death from desiccation. The springtime prevalence of soil-borne *Rhizoctonia* in these fallow fields indicates to what extent this fungus is able to persist in such field soils during the preceding summer." Variation in the prevalence of *R. solani* stem canker on potato crops *established from clean seed* was therefore attributed by ELMER to variation in saprophytic survival of *R. solani* in the soil, following potato harvest of the previous July. An annual survey of the incidence of stem canker in potato plots established from clean seed in some 15 scattered localities of eastern Kansas was made by ELMER during the 13-year period 1928-1940. A high percentage infection in any year could be correlated with the occurrence of soil conditions suitable for saprophytic survival of *R. solani* mycelium in the soil during July and August of the preceding year, *viz.* high rainfall, relatively low temperature, and absence of drying winds. Percentage infection was low, on the other hand, following a year in which July-August rainfall had been low, and hot drying winds had been frequent, leading to a drying-out of the surface soil. Variation in the incidence of stem canker from year to year was evidently not due to the effect of the current season's weather on development of infection, because *plants established from infected tubers showed a high percentage of infection throughout the whole period of the survey.*

Survival of *R. solani* on a host plant was not adversely affected by dryness of the soil in the summer months; if the land was occupied in August by a late-planted potato crop, or by some other crop susceptible to *R. solani,* then the potato crop of the following year showed considerable stem canker, regardless of weather conditions in the preceding July and August. From the results of these various experiments, ELMER concludes: "The prevalence of soil-borne *Rhizoctonia* in eastern Kansas can be approximately predicted from the relative soil moisture content of the preceding summer. . . . In regions like eastern Kansas, where soil-borne *Rhizoctonia* may periodically be practically eradicated because of environment, effective seed-potato treatments are valuable not only in preventing infection of the current season's crop but also in preventing reinfestation of the soil with this fungus."

*Fungi making no extensive saprophytic spread through the soil.*— A well-established example of this type of fungus is provided by *Fusarium culmorum,* the active saprophytism of which was shown by SADASIVAN (1939). Both natural, untreated wheat straw and straw sterilised in the autoclave were buried in 6 different types of soil for periods not exceeding 4 months; at intervals, samples of straw were removed from the soil, washed, and plated out after a light surface sterilisation with mercuric chloride. High percentages of *F. cul-*

*morum* colonies were obtained from the straws at many of the samplings; *F. culmorum* and *Penicillium* spp. were the dominant organisms forming colonies from the straws on the agar plates. SADASIVAN further demonstrated that the isolates of *F. culmorum* thus obtained possessed parasitic ability comparable to that of isolates derived from diseased plants, when tested against wheat seedlings.

SADASIVAN'S discovery was confirmed and extended by WALKER (1941), who demonstrated the saprophytic development of *F. culmorum* in straws buried in samples of soil taken from a number of fields at monthly intervals throughout the year. There appeared to be little correlation between percentage colonies of *F. culmorum* appearing on the isolation plates, and season or cropping history of individual fields. The relative numbers of colonies of *F. culmorum, Penicillium* spp. and other fungi obtained by WALKER were, however, greatly influenced by the surface sterilising agent employed and by the time of sterilisation; this suggested that a number of fungi were present in each straw, but that a "selection", which determined colony production on the agar plate (*see* above, p. 11), occurred during the surface sterilising and plating-out. Similar conclusions concerning the saprophytic ability of *F. culmorum* were reached by WEISE (1939) in his study of the foot rot of asparagus due to this fungus in Saxony. *F. culmorum* was invariably found to be present in samples of soil taken from the Weinböhla district, and was found living as a saprophyte both in compost heaps and in decomposing straw.

**Saprophytic Survival in Tissues Invaded as Parasite:** — Various more or less casual observations on the survival of root-infecting fungi in diseased crop residues have been reported. The longest survival periods have been recorded for mycelium in infected tree roots buried deeply in the soil; the most famous instance is provided by a much quoted piece of *Mesua ferrea* root infected by *Fomes noxius* which, according to TUNSTALL (1926), must have lain buried in the soil at the Tocklai Experiment Station in North East India for at least 14 years. COOLEY (1942) successfully isolated *Xylaria mali* from undisturbed roots of apple trees, affected by black root rot, at periods of 4 years and more after death of the host; he quoted a survival period of 16 years for another infection by the same fungus, as recorded by SCHNEIDERHAN (1936).

TAUBENHAUS and EZEKIEL (1930*b*) have drawn attention to the necessity for distinguishing between real and apparent saprophytic survival of a root-infecting fungus. These authors confirmed the earlier observation of TAUBENHAUS and KILLOUGH (1923) that the roots of cotton plants might live on underground throughout the Texas winter after the tops of the plants had been killed by frost. The root rot fungus, *Phymatotrichum omnivorum,* not only survived but also

spread along such living, overwintering roots; in one instance, TAUBENHAUS and EZEKIEL observed a spread of as much as 12 feet along a row of overwintering roots under dead tops. The viability of *P. omnivorum* on living overwintering roots was demonstrated by isolation of the fungus in pure culture, by its ability to put out fresh mycelial strands when the root was placed in a moist chamber, and by its rapid infection of cotton and turnip roots. No isolations were secured, on the other hand, from dead decaying roots, no strands were put out by the fungus, and no infection of healthy roots could be obtained by the use of such dead decaying roots as inoculum. TAUBENHAUS and EZEKIEL therefore concluded that, unless sclerotia were formed on the infected root, the fungus could not survive the winter on dead, decaying roots, but only on living overwintered ones. In confirmation of this claim, TAUBENHAUS and EZEKIEL cited an experiment in which they had successfully inoculated healthy cotton plants with tap roots of cotton plants killed by root rot only 1 day to 2 weeks earlier, but not with those of plants killed from 3 to 9 weeks earlier. NEAL and MACLEAN (1931) reported that mycelial strands of *P. omnivorum* recovered at various depths from the soil of infected cotton fields were viable as late as December, but that no viable strands could be found in January, February or March. More recently, EZEKIEL (1940) has shown that topping or girdling infected cotton plants at the advancing margins of root rot spots in midsummer may greatly shorten the survival period of *P. omnivorum* on the roots. From the practical point of view, however, interest in the saprophytic survival of *P. omnivorum* in dead infected root tissues has declined since the original announcement by KING and LOOMIS (1929) of their discovery of a sclerotial stage of this fungus in pure culture.

The survival of *Ophiobolus graminis*, causing the take-all disease of cereals, in infected plant tissues seems to have received greater attention than that of any other root-infecting fungus. The influence of soil conditions upon the survival period of *O. graminis* was examined by GARRETT (1938*b*, 1940), using a glass tumbler technique; at regular intervals, the viability of the fungus in 100 or more individual pieces of infected straw from each of the different soil series was ascertained by means of a wheat seedling test. From results thus obtained, GARRETT was able to correlate the rapidity of disappearance of the fungus with general microbiological activity of the soil; loss of viability was most rapid under conditions of medium to high temperature, suitable moisture content, and good soil aeration. Viability of *O. graminis* was preserved, on the other hand, at a low temperature (2°-3°C.) and in air-dry soil, and was actually maintained for longer in a water-logged soil than in one held at a moisture content of 50% saturation. Loss of viability was particularly hastened by the addition of fresh energy materials, poor or entirely lacking in nitrogen,

such as glucose, starch, or rye-grass meal, to the soil; this effect diminished as the nitrogen content of the material increased, so that rape dust with a nitrogen content of 5.8% was found to exert no significant influence upon the survival of *O. graminis* in the straws, whilst dried blood with a nitrogen content of 13% actually increased the survival period. Ammonium carbonate was found also to promote survival. GARRETT attempted to explain these results by the hypothesis that the "resting" mycelium of *O. graminis* in the infected wheat straw was subject to decomposition by the other micro-organisms of the soil; he suggested that the mycelium was attacked as a source of nitrogen by the micro-organisms decomposing the matrical straw (nitrogen content only 0.4 %). The addition of nitrogen-poor organic materials to the surrounding soil would enhance the nitrogen scarcity and increase the number of micro-organisms engaged in decomposition, whereas the addition of nitrogen-rich materials would provide an alternative and more readily available source of nitrogen than the mycelium of *O. graminis* for straw decomposition.

In a second paper, GARRETT (1940) reported survival of the fungus in almost 100% of infected straws buried for 8 months in a garden soil rich in humus and high in nitrogen content. Reconciliation of this observation with the hypothesis that the "resting" mycelium of the fungus was a passive subject for decomposition by the other soil micro-organisms was difficult, and led to further direct microscopical observation of the fungus in the infected straws. A slow but apparently continuous branching and development of the mycelium of *O. graminis* was found to occur for weeks or even months after the straws had been buried in the soil. At time of removal of the infected straws from the pure-culture flasks, the mycelium in the tissues was mainly of the hyaline type, corresponding to the "microhyphae" of FELLOWS (1928), but, after the straws had been buried in the soil, the dark mycelium, or "macrohyphae" of FELLOWS, developed. The development of dark mycelium was noticeably greater, and also more sustained, in the straws buried in soils well supplied with soluble nitrogen. GARRETT therefore concluded that survival of *O. graminis* depended upon the continued slow development of the mycelium inside the infected straw; a plentiful supply of soluble nitrogen from the soil prolonged this development, and thereby extended the life of the fungus. Some typical results obtained by GARRETT, which illustrate this important effect of nitrogen in prolonging the survival of *O. graminis* in the infected straw, are quoted in Table 9.

GARRETT therefore concluded that any treatment interfering with the supply of nitrogen from soil to straw might be expected to shorten the survival period of the contained fungus; treatments especially effective in this respect were incorporation of rye-grass meal in the

TABLE 9. *Percentage of straws containing viable Ophiobolus mycelium:* —

| SERIES | WEEKS | | | | | | |
|---|---|---|---|---|---|---|---|
| | 7 | 10 | 13 | 16 | 19 | 22 | 25 |
| No. 1, untreated soil ............. | 92 | 70 | 72 | 26 | 20 | 7 | 3 |
| No. 2, +1.56 mg. N ............. | 89 | 82 | 82 | 57 | 37 | 18 | 8 |
| No. 3, +3.125 mg. N ............ | 92 | 84 | 76 | 72 | 76 | 33 | 44 |
| No. 4, +6.25 mg. N ............. | 91 | 86 | 84 | 82 | 73 | 46 | 38 |
| No. 5, +12.5 mg. N ............. | 95 | 92 | 84 | 94 | 80 | 76 | 74 |

soil, and close crowding of the straws with a minimum of surrounding soil (Table 10).

TABLE 10. *Percentage of straws containing viable Ophiobolus mycelium:* —

| SERIES | WEEKS | | | | | | |
|---|---|---|---|---|---|---|---|
| | 3 | 6 | 9 | 12 | 15 | 18 | 21 |
| No. 1, 10 straws per 200 gm. soil ....... | 100 | 100 | 99 | 96 | 96 | 88 | 89 |
| No. 2, 50 straws per 200 gm. soil ....... | 100 | 99 | 99 | 98 | 91 | 91 | 84 |
| No. 3, 200 straws per 200 gm. soil ...... | 100 | 99 | 95 | 83 | 51 | 43 | 36 |

The survival of *O. graminis* in the infected plant tissues thus seems to depend especially upon its ability to form fresh hyphae. This, in turn, waits upon an adequate supply of nutrients; lack of nitrogen usually seems to be the limiting factor for *O. graminis,* as well as for other soil micro-organisms engaged in decomposition of the straw tissues. Now CHANG (1939) has shown that decomposition of composted wheat straw by a general soil flora proceeds substantially further in the presence of an adequate supply of phosphate, in addition to the usual supplement of nitrogen. Recent unpublished evidence suggests that the survival of *O. graminis* may be slightly prolonged by supplementary phosphate, if the straws are buried in a medium completely lacking this nutrient.

The gap between the conditions obtaining in such laboratory tumblers and those in soil *in situ* in the field has been bridged by the experiments of FELLOWS (1941), who followed the disappearance of *O. graminis in* naturally infected soil taken straight from the field and incubated under the eight possible combinations of high and low temperature, loose and firm packing, and moist and air-dry conditions. The low-temperature samples were stored in a deep cave and the high-temperature ones were kept in the glasshouse. Looseness was maintained by occasional stirring, and a firm packing achieved by thorough tamping of the soil whilst moist. The moist soils were maintained at approximately 60% of saturation, whereas the others were allowed to air-dry. Four experiments were made, and periods of incubation

varied from 230 to 777 days; at the end of the incubation period, all soil samples were brought to favourable tilth and moisture content, and a test crop of wheat grown in them to maturity, in the glasshouse. The degree of infection on the plants at harvest was expressed by means of a "severity rating". In almost every comparison provided by this series of extensive factorial experiments, the fungus disappeared more quickly in a warm soil than in a cold one, and more quickly in a loose soil than in a compact soil. The influence of moisture was less straightforward; under cool conditions survival appeared to be rather better in a moist than in a dry soil, whereas under warm conditions the reverse was the case. In all four series of experiments, without exception, disappearance of the fungus was most rapid in the warm, moist, loose soil, *i.e.* under just those conditions of high temperature, adequate moisture content and good aeration that were postulated by GARRETT (1938*b*) as most conducive to rapid loss of viability.

*Chapter 8*

# DORMANCY OF THE ROOT-INFECTING FUNGI

Specialisation of parasitism in a root-infecting fungus brings with it the hazard of local extinction when the infected host plant dies; the greater the degree of specialisation, the more remote is the chance that the parasite will be able to reach another susceptible host before the death of the first one. This hazard has been substantially reduced through the development of resting spores and sclerotia by many of the root-infecting fungi. Whereas long-lived resting spores are typically produced by members of the Phycomycetes, sclerotia are especially characteristic of the Ascomycetes and Fungi Imperfecti. By means of these organs, root-infecting fungi are enabled to survive for a period of years in the soil in the absence of a suitable host plant; a small proportion of such resting spores or sclerotia eventually re-establish the parasitic phase of the fungus, provided that sooner or later contact is made with the roots of a susceptible host.

**Resting Spores:** — The thick-walled resting spores of the Phycomycetes, resulting from the process of sexual reproduction, are responsible for long survival of the organisms in soil carrying no susceptible host plants. Thus SCHAFFNIT (1922) reported that potatoes contracted wart disease, due to *Synchytrium endobioticum,* on a plot that had been fallowed and kept free of weeds for no less than 10 years. A four-year rotation is frequently quite inadequate to control the clubroot disease of crucifers, due to *Plasmodiophora brassicae**; on Agdell field at the Rothamsted Experimental Station in England, which has been under a 4-course rotation of swedes with three non-cruciferous crops since 1848, a severe outbreak of clubroot first attracted attention in 1920. GIBBS (1939) has recorded survival of the resting spores of *P. brassicae* for 5 years in New Zealand, and FEDORINTCHIK (1935) in Russia obtained 27% infection in cabbage seedlings potted up in soil taken from a field not sown to crucifers for 7 years. GEACH (1936) found *Aphanomyces euteiches,* the cause of pea root rot, to survive for at least 2 years in pots of infected soil kept free of weeds. JONES and DRECHSLER (1925) secured field evidence that *A. euteiches* might survive under apparently non-susceptible crops for a period of 6 years, which was extended to 10 years by the survey of LINFORD and VAUGHAN (1925); later, however, LINFORD (1927) attributed these long survival periods to mild infections of the parasite in hosts other than pea. There is nothing inherently improbable in such long survival of resting spores in the soil, especially in view of the long survival of certain types of weed seed under suitable conditions. Nevertheless, when considering evi-

* This organism does not belong to the Phycomycetes, but to the Myxomycetes.

dence from length of crop rotation, it is unwise to exclude the possibility that weeds susceptible to the parasite may have established themselves at some time or other on the land, though it seems very unlikely that cruciferous weeds could have been responsible for the high percentage of infection reported by FEDORINTCHIK (1935), quoted above.

Scanty information is available concerning possible variation in survival of such resting spores under different soil conditions; such data as have been published have been derived from the field rather than from the laboratory. FEDORINTCHIK (1935) could detect no beneficial effect of ploughing fields two or three times a year in hasten-

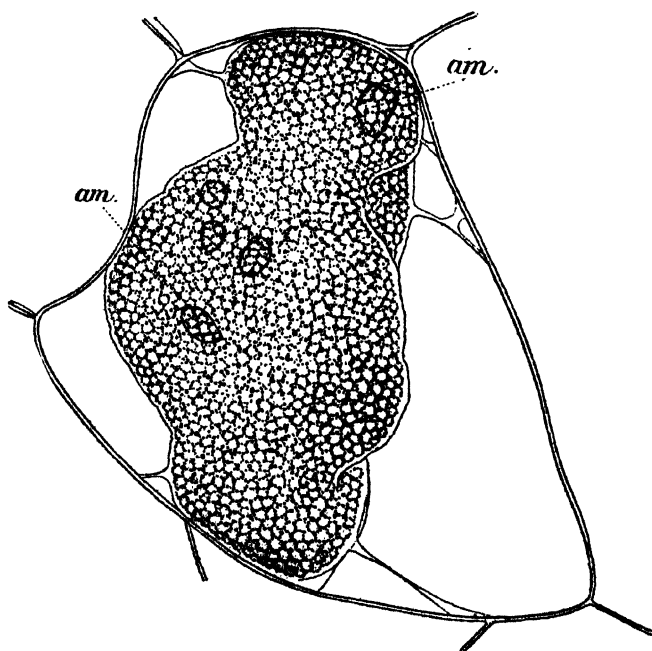



FIGURE 7.—Formation of resting spores of *Plasmodiophora brassicae* in cells of host. (*After M. Woronin*).

ing the disappearance of the clubroot organism from the soil in Russia, and GIBBS (1939) concluded that survival was influenced by the length but not by the type of rotation and management employed by farmers in New Zealand. In contrast to these field studies by FEDORINTCHIK and GIBBS, in which cruciferous host plants were used to detect viable spores of *Plasmodiophora brassicae* in the soil, BREMER (1923) developed a direct microscopical technique for the same purpose. Sections of infected cabbage roots containing spores of *P. brassicae* were buried in the soil, and viability of the spores was determined at inter-

vals by plasmolysis in salt solution, followed by deplasmolysis in water. Employing this technique, BREMER (1924) reported that a high proportion of spores germinated even in the soil freshly treated with lime, although germination was more rapid and more extensive in the acid, untreated soil. He found that injury to the spores through treatment with mercuric chloride, or through exposure to a temperature of 45°C., was least severe in the alkaline soil at *p*H 8.0, in which the dormancy of the spores was presumably more profound. As a result of this work, BREMER concluded that, in the absence of cruciferous host plants, *P. brassicae* was likely to survive for longest under those soil conditions, such as alkaline reaction, least favourable for spore germination. This important conclusion is likely to apply to the survival not only of other resting spores, but also of sclerotia, and even of mycelium in infected host tissue as well (*see* above, p. 66).

A direct microscopical method was also developed by GLYNNE (1926) for studying survival of the resting bodies (winter sporangia) of *Synchytrium endobioticum,* the fungus causing wart disease in potatoes. The sporangia were mounted in 1-2% aqueous acid fuchsin, and the thick brown sporangial walls were broken by pressure of the cover slip, so that the cell contents were expelled into the stain. The contents of living sporangia slowly assumed a pale pink colour, which gradually deepened; the contents of dead sporangia rapidly stained deep crimson. Whereas BREMER got over the difficulty of recovering the spores of *P. brassicae* from the soil by using sections of infected host tissue as a mount, GLYNNE solved the problem in another way, by extraction of the spores from soil with chloroform, which was found not to affect their viability. The complete method was apparently never employed by GLYNNE to study survival of *S. endobioticum* under different soil conditions, as her published experiments were concerned chiefly with determination of lethal temperatures *in vitro.* Both the Bremer and Glynne techniques, however, merit further consideration by investigators; although the resting bodies of these organisms survive for long periods in the soil, there must be a considerable reduction in numbers during the first few months, or even weeks, which could well be studied by such techniques.

Long-lived resting spores, or sporangia, of this type are characterised, as populations, by marked physiological heterogeneity. *Under no single set of soil conditions are all resting spores in a population likely to germinate.* Such physiological heterogeneity amongst populations of resting spores complicates the agricultural problem of eliminating them by cultivation or by other methods. Other things being equal, *the greater the physiological heterogeneity in a population of resting spores, the longer is the probable survival period of the parasite.* For this reason, the more rapid and diverse the fluctuations in the soil en-

vironment, the more extensively will resting spores germinate (and disappear from the soil in the absence of host plants). Factors especially likely to encourage germination are fluctuating soil temperature, moisture content, aeration and reaction; germination may also be stimulated by volatile substances emanating from plant residues buried in the soil, and from the roots of non-host as well as of host plants (NOBLE, 1924; PLATZ *et al.,* 1927).

Some information is available concerning the survival of spores of the cereal smut fungi in the soil; these spores are rather different from the thick-walled resting bodies of the Phycomycetes, and are less effective in securing prolonged survival of the fungus in soil, though fully effective in seed transmission of the organism. Thus in many parts of the world, soil infection by *Tilletia tritici,* causing bunt of wheat, is negligible, and satisfactory control is secured by seed treatment with a fungicide. In the Pacific Northwest of the U. S. A., however, considerable losses from bunt were reported by HUNGERFORD (1922) to follow contamination of fallows ready for autumn drilling of winter wheat, by clouds of bunt spores released during the threshing of crops on nearby fields. In a small plot experiment in which the soil was artificially inoculated with bunt spores, HUNGERFORD found the percentage of bunted heads to decrease from a maximum of 35 on the plot sown immediately after soil inoculation to a minimum of 4.5 on the plot sown a month later.

In similar small-scale plot experiments, HANNA and POPP (1934) found that percentage of bunted heads in spring wheat varied according to the type of inoculum mixed with the surface soil in the previous autumn; sifted bunt spores gave 11% of bunted ears, bunt balls gave 29%, and whole bunted heads gave 45%. Spore germination in the spring was found to be higher in spores taken from bunted heads overwintering on the surface of the ground than in those taken from buried overwintered heads. BORZINI (1935) reported that spores of *Ustilago zeae,* the maize smut, survived better on the surface of soil than when buried in the soil; the buried spores survived better in air-dry than in moist soil. Similar experiments on survival amongst spores of *Urocystis tritici,* causing flag smut of wheat, were carried out in Missouri by GRIFFITHS (1924). Diseased leaves were ground up, mixed with 2 parts of soil and placed in 2-inch flowerpots, of which half were buried 1 inch below the soil surface, and the other half 5 inches below. Samples of pots were taken at approximately fortnightly intervals from the beginning of January, and tested for viability of *U. tritici* by the planting of wheat seedlings, which were held in the glasshouse. The percentage of infected wheat plants thus obtained decreased markedly at successive samplings; survival of the organism was more prolonged in the pots buried more deeply.

**Sclerotia:** — Unlike resting spores, sclerotia are multicellular bodies, in which there is typically, though not always, differentiation of an outer skin or rind; this rind is assumed to exercise a protective function. The diameter usually varies from 0.5 to 2 mm., though a diameter of 1 cm. or more is sometimes encountered. The sclerotia of root-infecting fungi germinate to produce new vegetative mycelium; the minimum effective size of the sclerotium is determined by the volume of the food-base necessary for establishment by the fungus of root infection in the host. The most economical size of sclerotium for a root-infecting fungus may therefore be defined as the minimum effective size. The sclerotia of flower and foliage-infecting fungi, on the other hand, usually germinate to produce fruiting bodies, from which air-borne spores are ejected. The most economical size for sclerotia of this type is not necessarily the minimum effective size; in general, the sclerotia of the flower and foliage-infecting fungi are notably larger than those of the root-infecting fungi. Even the ergots of *Claviceps purpurea* are larger than typical sclerotia of most root-infecting fungi; the large sclerotia formed by species of *Sclerotinia* and *Botryis* are familiar to most mycologists. BROWN and BUTLER (1936) found sclerotia of *Sclerotinia sclerotiorum* to attain a length of 3 cm. on infected lettuce plants.

*The sclerotia of Phymatotrichum omnivorum.* — These have received more attention than those of any other root-infecting fungus. The sclerotia of *P. omnivorum* were discovered by KING and LOOMIS (1929) in laboratory cultures; they were first found in the field (in Texas) by NEAL (1929). This discovery of true sclerotia in *P. omnivorum* accounted for the longevity of the fungus under non-susceptible crops; this would otherwise have been difficult to reconcile with the demonstration by TAUBENHAUS and EZEKIEL (1930*b*) and by NEAL and MACLEAN (1931) that the vegetative strands of *P. omnivorum* do not survive for more than a few weeks on dead roots. Thus RATLIFFE (1934), ROGERS (1937), and REA (1939) have concluded that satisfactory control of cotton root rot is not given by rotations of less than 4 years' duration, or, in other words, by a break of less than 3 years under non-susceptible crops. The sclerotia usually vary in diameter from 1 to 2 mm., though a diameter of 1 cm. may be attained (ROGERS, 1937), and they are formed in chains on the vegetative strands. The histology of the sclerotia has been described by KING and LOOMIS (1929): "Microscopic examination of sections of the sclerotia showed that they were formed by the division and growth of the cells of portions of the large strands. This division of the cells apparently took place in the large central cells of the strands as well as in the smaller cells which surrounded the larger, as no continuous series of large cells of similar appearance extended through the sclerotia. Sections show that the interior of the sclerotia is made up of

closely packed, colorless, thin-walled cells of large and small size intermixed and varying in shape from roughly rounded to elongate oval and having no definite arrangement. A view of the surface of the sclerotia presents a labyrinthine appearance caused by the very irregular or contorted shapes of the brown, moderately thick-walled cells. From some of these surface cells, acicular hyphae, or setae, similar to those of the strands themselves, protrude at right angles, giving the sclerotia a somewhat bristly aspect under the microscope." The process of germination has recently been described in detail by PRESLEY (1939), and appears to be distinctly unusual. The new hyphae do not

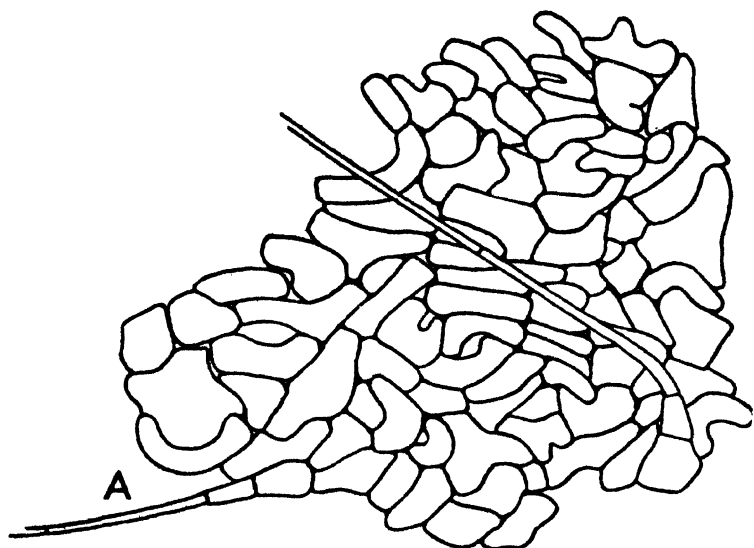



FIGURE 8. — Surface cells of sclerotium of *Phymatotrichum omnivorum.* Acicular hypha at A. (*After C. J. King and H. F. Loomis*).

arise as branches or elongations of the resting cells, but appear to be formed actually inside the cells, whose contents apparently go through a process of disorganisation and reorganisation that results in the formation of new hyphae, which eventually break through the old walls of the "mother cells".

*Distribution of sclerotia of P. omnivorum in the soil.* — Noteworthy studies on this aspect of the cotton root rot problem are those by KING and HOPE (1932) and by MCNAMARA and HOOTON (1933). KING and HOPE found sclerotia abundant under cotton at depths between 12 and 24 inches, being most numerous between 16 and 20 inches. Under alfalfa they were abundant between 6 and 30 inches, and most numerous between 12 and 18 inches. Under a Chinese elm, sclerotia were found at levels ranging from 6 to 48 inches.

McNamara and Hooton made numerous excavations around the first cotton plants to die of root rot after 3 or 4 years of clean fallow or non-susceptible crops, on the assumption that such plants represented primary infections. Most of these primary infections were successfully traced either to sclerotia, or to infected plant material. McNamara *et al.* (1934) later reported that sclerotia were not invariably the source of primary infections, many of which were traced to "persistent strands". Such strands were described as reddish to dark brown in colour, in contrast to the buff or light brown colour of the strands on the still living host plant; the persistent strands were also smooth, having lost the mantle of acicular hyphae that gives the active strands their characteristically fuzzy appearance. Such persistent strands were sometimes found upon the decaying remains of old cotton roots; at other times they occupied empty root channels. Primary infections in cotton after 2 years of oats were traced to such persistent strands, which were also found interlacing a colony of sclerotia in a plot that had been under fallow for no less than 5 years. In the latter instance, the strands may have arisen through germination of the sclerotia at any time during the 5-year period; the sclerotia associated with this and other primary centres of infection in the first cotton crop after the 5 years fallow may also have been of secondary origin, through a process of "sclerotial budding", such as was described by King *et al.* (1931).

At first sight, these observations of McNamara *et al.* (1934) upon the persistent strands may seem difficult to reconcile with those of Taubenhaus and Ezekiel (1930*b*) and Neal and Maclean (1931) on the very limited survival of vegetative strands upon plants just dead from root rot. The persistent strands, however, are probably more akin to sclerotia than to the ordinary vegetative strands; the sclerotia themselves, moreover, are merely a specialised development of the vegetative strands, upon which they arise. Development either of sclerotia or of the persistent type of strand may be associated with a decline in nutritional level of the mycelium after a period of abundance; thus King and Loomis (1929) first observed formation of sclerotia on strands that had grown out from infected cotton roots into the surrounding moist sand in which the roots were buried. McNamara and Hooton (1933) reported, moreover, that they did not find sclerotia on the tap roots or larger lateral roots of cotton plants, but out in the soil where only small rootlets occurred. It is pertinent to recall at this point that the studies of Taubenhaus and Ezekiel (1930b) were carried out with the tap roots and larger lateral roots of infected plants.

McNamara and Hooton (1933) stressed the fact that in their excavations of primary centres of infection, they found no sclerotia in plots planted each year to cotton, whereas they were abundant under

cotton following non-susceptible crops or fallow; they concluded, therefore, that the sclerotia "are connected primarily with the saprophytic phase of the fungus and serve as a resting stage". ROGERS (1937), employing a highly effective method for separating sclerotia of *P. omnivorum* from the soil (ROGERS, 1936), obtained, on the other hand, higher numbers of sclerotia under continuous cotton than under cotton or any other crop in a 4-year rotation of cotton with 3 non-susceptible crops (*see* Table 11, constructed from ROGERS' data).

TABLE 11. *Number and viability of Phymatotrichum omnivorum sclerotia in a 4-year rotation as related to time interval since last planting of cotton:* —

| TIME INTERVAL | NO. OF SCLEROTIA | NO. OF VIABLE SCLEROTIA | PER CENT VIABLE SCLEROTIA |
|---|---|---|---|
| *End of cotton year*........................ | 4488 | 1665 | 37.1 |
| *End of first year under non-susceptible crop*... | 9201 | 5765 | 62.7 |
| *End of second year under non-susceptible crop* | 2681 | 1479 | 55.2 |
| *End of third year under non-susceptible crop*.. | 1617 | 560 | 34.6 |
| *Continuous cotton* ........................ | 10,500 | 6959 | 66.3 |

ROGERS' data do, however, tend to confirm the claim made by MCNAMARA and HOOTON that formation of sclerotia occurs after parasitic activity has ceased; the highest sclerotial population, and the greatest percentage viability of sclerotia in the population, was found by ROGERS to occur not at the end of the cotton year, but at the end of the first year under a non-susceptible crop. In a laboratory study, ROGERS (1939) found that in Houston black clay soil (saturation capacity 70%) sclerotia were produced at moisture contents ranging from 21 to 43% saturation, with an optimum moisture content at 36% saturation. The temperature range for production of sclerotia was found to be 11°-37°C., with an optimum at 27°C.

*Longevity of sclerotia of P. omnivorum in the soil.* — The sclerotia of *P. omnivorum,* like the strands, are very sensitive to desiccation; KING *et al.* (1931) found them unable to survive drying for 1¼ hours in the air of the open laboratory. Other sclerotia kept under distilled water gave 81% germination after 92 days, and 20% germination after 121 days. The susceptibility of the sclerotia to desiccation has been confirmed by TAUBENHAUS and EZEKIEL (1936) and by KING and EATON (1934) in experiments on survival and germination of sclerotia in soil at different moisture contents. TAUBENHAUS and EZEKIEL studied loss of viability in sclerotia kept in Houston clay soil (saturation capacity 70% moisture) maintained at different moisture contents in small, stoppered glass vials; 25 sclerotia were placed in the soil of each vial. Germination was tested 9 days after setting up the experiment and subsequently at yearly intervals; 50 sclerotia were appar-

ently selected from the 75 sclerotia originally placed in 3 vials. No sclerotia from the air-dry soil germinated at the first test, 9 days after setting up the experiments, or at any subsequent test. None of the sclerotia buried in the soils maintained at 14%, 71% or 86% saturation was viable at the end of the first year; some of the sclerotia buried in the soils at intermediate moisture contents, *viz.* 29%, 43% and 57% saturation, survived the whole test period of 5 years, viability at the final test ranging from 10 to 16%. EZEKIEL (1940) has since reported that mean germination was 10% after 6 years, and 8% after 7 years, but that no germination was obtained after 9 years or more.

Now survival of sclerotia depends upon two contingencies (i) that the sclerotia do not germinate and dissipate themselves as mycelium (ii) that they retain their capacity for germination. Since TAUBENHAUS and EZEKIEL apparently selected 50 out of 75 sclerotia for their germination test, it is not possible to estimate from their table of data how many of the sclerotia were lost through germination or decay, but the proportion evidently did not exceed one third. The conditions of reduced aeration in the stoppered vials might have been expected to reduces spontaneous germination of the sclerotia; conditions of reduced aeration might also be deduced from the more rapid loss of viability in sclerotia kept in the two wettest soils.

In the experiments of KING and EATON (1934), on the other hand, disappearance of sclerotia through germination was much more frequent. Their experiment was carried out in a coarser-textured soil — Gila fine sand (saturation capacity 27% moisture) — in open containers; aeration conditions were obviously much better than in the stoppered vials used by TAUBENHAUS and EZEKIEL. The test was set up in May and the sclerotia were buried in the soil inside cheesecloth bags, for easier recovery, but in spite of this precaution KING and EATON remark: "Most of the cheesecloth bags had become badly decomposed by December, and many of the sclerotia having germinated in place, it became increasingly difficult to recover the desired numbers for making the monthly viability tests." Survival in air-dry soil was better than that in the experiment of TAUBENHAUS and EZEKIEL; 15% of sclerotia were viable after 2 months, though none after 3 months. In the soil held at 19% saturation, 33% sclerotia were viable after 2 months, but none after 3. There was not much difference in rate of loss of germinability amongst sclerotia recovered from the three wettest soils, held at 37, 93, and 100% saturation; germination varied from 10 to 18% at the 12 months test.

A comparison of the results obtained by KING and EATON with those of TAUBENHAUS and EZEKIEL thus indicates the great importance of spontaneous germination as a factor reducing survival of sclerotia. The factors affecting survival of *P. omnivorum* sclerotia have been analysed with considerable ingenuity by MITCHELL *et al.*

(1941). These authors found in laboratory experiments that the percentage of sclerotia recoverable from the soil was greatly reduced by the addition of 3% ground organic materials, such as farmyard manure, cotton seed meal, cotton roots, sorghum, alfalfa or straw to the soil; these reductions in numbers of sclerotia occurred chiefly in the first two weeks' incubation in the organic-amended soils, and hence coincided with the period of most active decomposition of the organic material. Since observations made on Rossi-Cholodny slides suggested that this rapid disappearance of sclerotia was due chiefly to germination, an experiment was planned in which the recovery of germinable sclerotia was compared with that of non-germinable sclerotia. Two lots of sclerotia were available, *viz.* young sclerotia (80% germinable) and old sclerotia (50% germinable). Half of the sclerotia in each batch were killed by heating to 85°C. for 5 minutes. Ten sclerotia were buried in each container at known locations on glass slides, so as to facilitate recovery. The numbers of sclerotia eliminated from each of 5 series of soils, *viz.* untreated, + 1% superphosphate, and + 3% chopped green alfalfa, straw and farmyard manure, respectively, are given in Table 12, which is taken from MITCHELL *et al.*

TABLE 12. *Percentage of viable and killed sclerotia eliminated* from soil receiving different treatments:* —

| SOIL TREATMENT | YOUNG SCLEROTIA LIVING | YOUNG SCLEROTIA KILLED | OLD SCLEROTIA LIVING | OLD SCLEROTIA KILLED |
|---|---|---|---|---|
| | Percent | Percent | Percent | Percent |
| *Untreated (check)* | 20 | 5 | 15 | 0 |
| *Superphosphate* | 5 | 0 | 10 | 0 |
| *Ground straw* | 70 | 15 | 50 | 15 |
| *Ground alfalfa* | 75 | 30 | 40 | 25 |
| *Manure* | 75 | 40 | 15 | 5 |

From these results, MITCHELL *et al.* concluded that germination was one of the factors contributing to the disappearance of the sclerotia in the soils treated with fresh organic material. The living sclerotia disappeared much more rapidly than the killed ones, and the young ones (80% germinable) more quickly than the old ones (50% germinable). Even the killed sclerotia disappeared more rapidly from the organic-amended than from the untreated soil, however; MITCHELL *et al.* comment upon this as follows: "It is not known why heat-killed sclerotia are more rapidly eliminated from organic-amended soil during the early period of incubation. It is possible that a mass-inoculation effect with more numerous and perhaps more diverse soil micro-

* See list of errata for volume 63, J. agric. Res., for correction of error in original heading of this Table.

organisms is obtained; it is also possible that the sclerotial substance presents a source of supply of one or more elements required during the initial decomposition stages of the added organic material by the soil microflora concerned."

CLARK (1942), who was one of the co-workers in MITCHELL *et al.*, later reported further experiments of this type, but on a more extensive scale, with the sclerotia of *P. omnivorum*. In a similar but larger experiment comparing rates of disappearance of viable *versus* heat-killed sclerotia, conditions were more favourable for decay of the dead sclerotia than for germination of the living ones; the influence of microbiological activity in accelerating disappearance of both living and dead sclerotia was demonstrated by a comparison between rates of disappearance of surface-sterilised sclerotia buried in sterile soil, on the one hand, and of untreated sclerotia in unsterilised soil, on the other. The effect of organic materials in accelerating rate of disappearance of viable sclerotia was once again demonstrated, and was shown to increase with rising soil temperature, and with increase in moisture content of the soil. The effect also varied with soil reaction, being greater in an acid-treated soil of *p*H 3.0 and in a limed soil of *p*H 7.9 than in the untreated soil, or in the same soil receiving smaller doses of acid; the effect was more pronounced in sclerotia buried at some depth in the soil than in those buried near the surface.

These and other results obtained by MITCHELL *et al.* and CLARK help to elucidate the controlling effect of organic manures upon cotton root rot (KING *et al.*, 1934*a*), which is especially pronounced when such manures are applied some months in advance of sowing time (KING, 1937). MITCHELL *et al.* also reported a field experiment on land heavily infected with *P. omnivorum*. The usual late autumn ploughing in preparation for spring sowing of cotton was compared with deep rotary tillage carried out in early autumn (Oct. 3*rd*); of the three rotary-tilled areas, the first received nothing, the second farmyard manure, and the third sorghum fodder. In August of the following year, excavations were made under the cotton crop to determine the relative abundance of sclerotia in the different areas. Sclerotia were not found in the upper 12 inches of soil in any of the areas that had been rotary tilled, though they were present below the 12 inch level; sclerotia were abundant, however, between the 6 and 12 inch levels in the control area that had received the usual late autumn ploughing. Percentage mortality amongst the cotton plants on the variously treated plots is given in Table 13, taken from MITCHELL *et al.*

*Sclerotia of other root-infecting fungi.* — Working with another sclerotium-forming fungus, *Sclerotium rolfsii*, LEACH and DAVEY (1938) obtained good correlation between numbers of viable sclerotia and incidence of root rot in the sugar-beet crop. They found approximately 80% of the sclerotia to occur in the upper 6 inches of soil, and

TABLE 13. *Percentage mortality in cotton due to root rot (Phymatotrichum omnivorum)* : —

| | PLOUGHED | DEEP ROTARY TILLAGE | ROTARY TILLAGE+ FARMYARD MANURE | ROTARY TILLAGE+ SORGHUM FODDER |
|---|---|---|---|---|
| Sept., 1939 (in crop preceding the experiment) .......... | 85.3 | 80.0 | 96.0 | 74.0 |
| August, 1940 ................ | 90.0 | 36.3 | 7.0 | 20.0 |
| October, 1940 ............... | 94.0 | 69.0 | 34.0 | 60.0 |

less than 2% of the sclerotia below 12 inches; soil sampling for sclerotia to a depth of 8 inches was accordingly considered adequate. An immediate practical use was found for this method of sampling for the sclerotia of *S. rolfsii*, by means of which probable losses from root rot in the next beet crop could be predicted; if probable loss exceeded an agreed level, the grower could be advised to substitute another crop for beet. The figures of LEACH and DAVEY showed a comparatively rapid decline in the population of viable sclerotia under a crop non-susceptible to this fungus; numbers were commonly reduced to one third or one quarter of the original population in an interval of 6 months, and in one instance numbers were reduced from 4810 in December to 150 (viable sclerotia per sq. foot of soil to a depth of 8 inches) in the following July.

The formation of sclerotia by *Rhizoctonia solani* in pure culture under different conditions of nutrition, temperature, atmospheric humidity, reaction of the medium, etc. has been studied by TYNER and SANFORD (1935); the optimum temperature for sclerotial production was found to be 18°-21°C. which is lower than that for *rate* of mycelial advance (*circa* 25°C.). Formation of scelerotia was favoured by high atmospheric humidity, but was not greatly reduced even by a humidity as low as 31%. In respect of their toleration of desiccation, the mature sclerotia of *R. solani* afford an interesting contrast to those of *Phymatotrichum omnivorum*. Thus PALO (1926) found them to survive for longer in air-dry than in moist soil, and GADD and BERTUS (1928) recorded survival of sclerotia stored dry in a corked tube in a Ceylon laboratory for 6 years.

*Chapter 9*

# CONTROL OF ROOT DISEASE IN FIELD CROPS: CROP ROTATION

The problems of root disease control in field crops are perhaps more interesting, because more diverse, than those involved in the culture of either plantation or glasshouse crops. In plantation cropping, the grower is usually concerned with a single crop, to the needs of which everything can be subordinated, as in a factory for the mass production of a single article. In commercial glasshouse practice, again, the grower is often engaged in production of only a single major crop, or perhaps two. In field cropping, on the other hand, the farmer is generally concerned not only with a rotation of three, four, or more crops, but also with the maintenance of stock as well. Any measures that are suggested for control of a soil-borne disease affecting a single crop have therefore to be considered in relation to their effect not only upon that particular crop, but also upon the other crops in the rotation and upon the maintenance of stock as well. Needless to say, the farmer will adopt those control measures that involve minimum expense and interference with his established routine; control of soil-borne diseases must therefore be sought rather through improvement of general farming policy than through expensive special operations. Above all, the effectiveness of crop rotation in keeping the great majority of soil-borne diseases and pests within bounds must be held responsible for the stillbirth of many ingenious schemes for root disease control. Again, whereas the soil and aerial environment of the crop can be directly controlled in glasshouse practice, in the field control of the crop's environment must usually be indirectly sought.

Control measures employed against soil-borne diseases of field crops will be classified and discussed, in this and the two following chapters, under the following heads:—

(i) crop rotation
(ii) plant sanitation
(iii) disease control under the growing crop.

Crop rotation is the basis of root disease control for field crops; plant sanitation is concerned with elimination of the parasite before the next susceptible crop is grown; disease control under the growing crop comprises all those palliative measures designed to minimise loss arising from sources of infection that have escaped the sanitary measures.

**Crop Rotation:**—Crop rotation is the oldest and most effective method of root disease control in field crops; its origins are a matter for the agricultural historian, but its mechanism still presents to the plant

pathologist some interesting problems, the existence of which has only recently come to be realised. The effectiveness of crop rotation depends upon specialisation of parasitism in the soil-borne parasites, amongst which may be included not only fungi and a few plant-pathogenic bacteria, but also plant-attacking nematodes as well; the very primitive parasites that are not limited in this way by their host range are limited in other ways, and so do not seriously impair the effectiveness of crop rotation for root disease control.

The efficiency of crop rotation as a root disease control measure may be defined as varying inversely with the length of rotation necessary to obtain adequate control of the particular disease. Adequate control does not imply complete elimination, but simply reduction of the parasite to a low level, at which it causes commercially negligible reduction in yield of the host crop. Rotation is most effective in control of root diseases caused by those highly specialised root-infecting fungi that have only a limited power of saprophytic survival in infected host tissue, and do not form resting spores or sclerotia. It is much less effective against fungi producing resting spores or sclerotia at conclusion of their period of parasitic activity; highly specialised parasites of this type present the most difficult problem of all. The efficiency of rotation for root disease control also decreases as the saprophytic capacity of the parasite increases; the requisite length of rotation is inevitably prolonged by ability of such a facultative saprophyte to compete with obligate saprophytes for colonisation of virgin crop residues. Fortunately, however, this faculty of active saprophytism is possessed by such fungi at the expense of their parasitic capacity, so that these fungi are not so difficult to control as the more highly specialised parasites forming resting spores or sclerotia.

*Elimination of fungi surviving only as mycelium inside infected host tissues.* — *Ophiobolus graminis,* causing the take-all disease of cereals, is a fungus with a strictly limited power of saprophytic survival, in tissues invaded as a parasite (*see* above, p. 66); from an examination of all available published evidence, Garrett (1942) has concluded that a one-year break under any non-cereal crop except pasture will give adequate control, though occasionally the disease may cause serious trouble in a two-course rotation such as that of sugar-beet and barley. Outbreaks of take-all in a cereal crop grown in two-course rotation are probably limited to light-textured, alkaline soils exceptionally favourable to underground spread of the fungus along the roots of the host crop; in such soils, the small amount of inoculum remaining after the one-year break is much more dangerous than in heavier or more acid soils, in which the fungus spreads more slowly along the roots. As Garrett has pointed out, adequate control of take-all, and not complete elimination of *Ophiobolus graminis* from the soil, is the object of crop rotation; complete elimination of this

fungus from the soil is not achieved even by a two-year break under fallow or a non-susceptible crop.

Another fungus that seems to have a strictly limited term of survival in tissues invaded as a parasite is *Verticillium albo-atrum*. Thus in field experiments on control of the potato wilt due to this fungus, McKAY (1926) found adequate control to be given by a three-year rotation of potatoes with grain and clover (4% infected tubers), though not by a two-year rotation of potatoes with grain (22% infected tubers); under continuous potatoes, there were 34% infected tubers. In another experiment, the percentages of infected tubers in potato crops grown under rotations of 1-4 years duration were 25, 21, 1 and 0.3, respectively. A rather similar range of infection was obtained by ZELLER (1936) in rotations designed for control of blue stripe wilt, due to *V. albo-atrum*, in black raspberries. The percentages of infected plants in raspberries grown under rotations of 1-4 years were 38, 21, 2.5 and 1.0, respectively. McKAY remarked upon the discrepancy between his cultural tests for recovery of *V. albo-atrum* from infected potato haulm buried in the soil, and the results of his rotation experiments; the fungus was isolated from the infected haulms in May, after they had lain in the soil over winter, but not in May of the following year. ZELLER buried a number of 10-inch sections of infected raspberry canes 6 inches deep in the soil at the end of October, 1927, and periodically attempted to isolate the fungus from each of 15 cane sections recovered from the soil at successive samplings. The proportion of successful isolations varied as follows: February 1928 — 15/15, May 1928 — 12/15, October 1928 — 6/15, and February 1929 — 0/15. Had McKAY and ZELLER used the host plant instead of the agar plate as the ideal test for survival of *V. albo-atrum* (admittedly a difficult proposition with this fungus), the discrepancy between these tests and the results of their rotation experiments would probably have been diminished (*see* above, p. 12).

*Elimination of fungi surviving as resting spores.* — The resting spores of most cereal smut fungi have a relatively short life in the soil; adequate control of the kernel smuts is usually provided by seed disinfection, as soil contamination generally occurs only through liberation of spore clouds during threshing. Such soil contamination by the spores of *Tilletia tritici* was reported by HUNGERFORD (1922) to cause losses of as much as 85% through bunt in the Pacific Northwest of the U. S. A.; losses of this order through soil infection by bunt spores are fortunately rare. Disappearance of free and unprotected smut spores from the soil seems to be very rapid, whether through germination or through death and decay; spores protected by enclosing host tissues have a better chance of survival (HANNA and POPP, 1934). Whereas crop rotation is usually unnecessary for control of soil infection by the kernel smuts, it may be essential for control of the leaf smuts, because

infected crop residues are turned into the soil; the spores of such leaf smuts enjoy the protection of enclosing host tissues. Thus *Urocystis tritici,* causing flag smut of wheat, was found by GRIFFITHS (1924) to survive for a year in a small plot originally heavily contaminated by the digging-in of infected wheat straw; 9/377 (2.4%) test wheat plants became infected. A very similar result was later obtained by TISDALE *et al.* (1927). Nevertheless, under ordinary farm practice, a one-year break is usually sufficient to keep the flag smut disease under control.

Another parasite that persists in the soil only in the form of resting spores, but has a greater power of prolonged survival, is *Plasmodiophora brassicae,* causing clubroot of crucifers. Although FEDORINTCHIK (1935) has reported that this organism survived in a heavily infected field for 7 years and then caused 27% infection of potted cabbage seedlings, this is probably an extreme case, and rotations of shorter duration than this period usually give adequate control of the disease in practice. Four-year rotations, in which cruciferous crops are kept off the land for three years, are sometimes adequate, but a five-year rotation is usually found to be the minimum that can safely be employed. A shorter rotation than this may appear to control the disease on land that carries only a small population of *P. brassicae,* but may result in a gradual accumulation of this parasite in the soil; this is often overlooked until a fairly serious outbreak of clubroot has occurred. According to FEDORINTCHIK (1935), a high concentration of spores in the soil is required before severe clubbing can occur. As with the take-all disease of cereals, the length of rotation required to keep clubroot under control can probably be correlated with suitability of the soil for parasitic activity; in alkaline soil, a much higher concentration of the organism is required for successful establishment of infection than in acid soil.

Another soil-borne parasite perpetuated by means of resting spores is *Aphanomyces euteiches,* which causes root rot of peas. GEACH (1936) found this fungus to survive for at least two years in pots of soil kept fallow and free of weeds. Field evidence at first suggested a much longer survival period; out of 9 fields that had not carried diseased peas for 10 or more years, three were found by LINFORD and VAUGHAN (1925) to be suffering from widespread and severe root rot. Later, however, LINFORD (1927), commenting upon the wide host range of *A. euteiches,* suggested that the fungus might be carried over these long periods in between two pea crops as a weak parasite on the roots of apparently resistant crops, and on those of weeds; he also reported a serious incidence of this disease in some crops sown on virgin land.

*Elimination of fungi surviving as sclerotia.* — Cotton root rot in the U. S. A., due to *Phymatotrichum omnivorum,* furnishes the most

outstanding example of an important root disease in which the length of rotation necessary for control has been correlated with longevity of the sclerotia in the soil (*see* above, p. 77). RATLIFFE (1934), ROGERS (1937) and REA (1939) agreed that a two-year rotation exercised no check upon the disease at all, that a three-year rotation reduced it somewhat, but that for satisfactory control a four-year rotation had to be followed. Even a four-year rotation by no means prevented the appearance of root rot, but by reducing the number of plants affected, and especially by delaying the development of the disease until later in the cotton season, the four-year rotation markedly reduced losses in yield due to root rot.

*Elimination of facultative saprophytes.* — Next may be considered those diseases caused by organisms with greater saprophytic potentialities. Little precise information is to be found concerning the saprophytic life of *Actinomyces scabies* in the soil, but the relatively long rotation required for control of potato scab suggests that the organism may survive as a saprophyte in the soil, independently of infected potato tissue. GOSS and AFANASIEV (1938) have discussed the incidence of scab in rotation experiments carried out under irrigation in Western Nebraska; two-year rotations failed to reduce the disease at all (and indeed it was worse in such rotations than under continuous potatoes), a three-year rotation appreciably reduced it, and four- to six-year rotations gave satisfactory results, eliminating the severe form of scab, and giving the highest proportion of sound, unmarked tubers.

Another disease of the potato in which free saprophytic survival of the causal fungus may complicate control by rotation is stem canker and tuber scurf, due to *Rhizoctonia solani.* BLAIR (1943) has shown by laboratory experiments that this fungus can grow through untreated field soil as a saprophyte, though its activity is depressed by addition of 1% or more of ground dried green manure, apparently through the competition of other micro-organisms better fitted to attack the organic material. Although the superficial tuber scurf form of this disease is caused by the formation of sclerotia, these bodies are often little more than mycelial plates, nor do they show any tissue differentiation; the part that they play in determining survival of *R. solani* in the field cannot as yet be estimated. SANFORD (1939) remarked that, in some areas of Alberta, a year's summerfallow gave no appreciable control of the tuber diseases due to *R. solani* and *A. scabies.* Nevertheless, GOSS and AFANASIEV (1938) found a marked reduction in incidence of tuber scurf under two-year rotations in Western Nebraska, as compared with that under continuous potatoes, and a four-year rotation reduced it to a negligible minimum. BLODGETT (1939) reported incidence of tuber scurf in New York State to be markedly reduced by a two-year rotation, as compared with con-

tinuous potatoes, but it did not seem to be further diminished by a five-year rotation. Goss and Afanasiev, and Blodgett, observed incidence of tuber scurf to be substantially reduced both by farmyard manure and by a green manure cover crop; it is tempting to correlate this observation with the results obtained by Blair, but it must be noted that Blodgett also found a reduction in incidence of tuber scurf to follow the application of an artificial fertiliser.

The foot rot of cereals due to *Fusarium culmorum* is well known to be less amenable to control by crop rotation than is the take-all disease; Sanford (1939) has commented upon this fact: "For example, one asks why one year of summerfallow produces such a marked effect in reducing the damage of *O. graminis* in the wheat crop following it, but gives much less control of *H. sativum* and *F. culmorum,* no control of *Pythium* sp., and in certain areas at least, no appreciable control of the potato diseases caused by *A. scabies* and *R. solani.*" An explanation of this difference in behaviour is perhaps afforded on the one hand by the findings of Garrett (1938*b,* 1940) concerning the limited power of survival of *O. graminis,* in tissues invaded as a parasite, and on the other by the demonstration by Sadasivan (1939) and Walker (1941) that *F. culmorum* can actually invade fresh wheat straw buried in the soil, as a free-living saprophyte. The foot rot of cereals due to *F. culmorum* is of little cosmopolitan importance, as compared with the take-all disease, but in Canada conditions seem to favour the parasitism of this fungus upon wheat; in combination with *Helminthosporium sativum,* it causes serious losses. In view of the widespread distribution of *F. culmorum* in the wheat-growing soils of other countries, its failure to act at all commonly as a serious parasite of wheat elsewhere than in Canada requires further investigation.

For certain other root-infecting fungi, apparent survival periods of such length have been reported that, if the complete absence of host plants in the interim period can be confirmed, the parasites must be regarded also as saprophytes of *soil inhabitant* status. For example, Barker (1923) reported that it was frequently impossible to grow flax varieties susceptible to wilt (*Fusarium lini*) more than once every 10-12 years on the same land, and Melhus *et al.* (1926) found the cabbage yellows organism, *Fusarium conglutinans,* to last for at least 11 years in the soil; a survival period of 14 years under grass had previously been reported by Jones and Gilman (1915) for the same fungus, which was responsible for a severe outbreak of yellows in the first cabbage crop planted on the ploughed-up sod. It is known, however, that *Fusarium lini* can be seed-borne, so that this may explain the occurrences cited by Barker; Baylis (1940), reporting survival periods of 8 and 11 years in the absence of flax crops in New Zealand, took note of this possibility of seed transmission by

observing that: "The seed came from crops in which no wilt was discernible, and the great majority of crops raised from it showed no sign of the disease." Before such long periods of survival by a parasite in between one susceptible host crop and the next can be accepted as evidence of its capacity for indefinite saprophytic survival in the soil, it is necessary to exclude possibility of seed transmission. Again, LINFORD's (1927) suggestion, made in connection with the long apparent survival periods of *Aphanomyces euteiches,* that a fungus may survive as a weak parasite on the roots of apparently immune crops (*i.e.* showing no disease symptoms above ground), or on those of weeds, deserves wider consideration. The need for experimental investigation to supplement such field records as those just cited is thus very apparent.

*Other effects of crop rotation upon survival and activity of root-infecting fungi.* — So far, only the obvious and well-established effect of crop rotation upon the numbers of a parasitic organism in the soil has been considered; the numbers of the parasite increase with the frequency of host crops. Little attention has yet been paid to the relative effect of different non-host plants upon the survival of a parasite. Data have recently been provided by BOSE (1938) in India which suggest that the incidence of root-disease in a crop may be profoundly affected by the nature and sequence of preceding crops in the rotation, even though none of these crops can act as host plants to the particular parasite concerned. BOSE demonstrated that incidence of wilt, due to *Fusarium vasinfectum,* in pigeon pea was significantly less after a crop of tobacco than after one of linseed or fallow. The design of the experiments failed to permit discrimination between the effect of the living roots of the preceding crops and that of the crop residues. This result was consistently obtained in experiments carried out in three consecutive seasons, and appeared both on naturally-infected plots, and on plots in which the natural inoculum had been artificially reinforced.

In pot experiments, HILDEBRAND and WEST (1941) found that the growth and turning-under of several consecutive crops of soybeans markedly reduced the incidence of Ontario root rot (the etiology of which is still incompletely understood) in strawberries; the growth of red clover cover crops, on the other hand, produced no such beneficial effect. WEST and HILDEBRAND (1941) discovered that this beneficial effect of soybeans in reducing root rot could be simulated by addition of glucose to the soil. Later RICHARDSON (1942), working in the same laboratory, reported that the growth and turning-under of four successive crops of soybeans in pots reduced the incidence of root rot, due to species of *Pythium, Helminthosporium,* and *Fusarium,* in corn seedlings; a succession of red clover cover crops, on the other hand, produced no comparable improvement in the health of the roots of the following corn crop.

A more prolonged survival of the take-all fungus in infected wheat stubble in fallow soil than in soil under crop has been reported by GARRETT (1943). Eight weeks after burial of the pieces of infected straw in the soil, 68% of those from the fallow soil contained viable mycelium of *Ophiobolus graminis,* but only 18, 17 and 4% of those from soil under trefoil, mustard and oats, respectively. GARRETT attributed the more rapid disappearance of *O. graminis* from soils under crop to competition between the take-all fungus and plant roots for the limited supply of available nitrogen (*see* above, p. 67). He suggested that this observation might explain the success of a system followed by certain English farmers for continuous barley growing. Barley is susceptible to the take-all disease, and the second or third barley crop on the same land is sometimes severely attacked. But barley undersown with trefoil (which makes a luxuriant growth in late summer and autumn after the barley has been cut, and is then ploughed in as a preparation for the next barley crop) had not thus far been observed to suffer from take-all. To account for this observation, GARRETT supposed that the active growth of the legume after harvest kept the available nitrogen content of the soil at a very low level, with resulting detriment to the longevity of *O. graminis,* most of which was unable to survive until sowing of the new barley crop in the spring.

The effects of crop growth upon the soil are many and diverse; one crop differs from another not only in its effect upon the micro-biological equilibrium of the soil, as HILDEBRAND and WEST (1941) and WEST and HILDEBRAND (1941) have so extensively demontrated, but also in its demands upon reserves of plant nutrients. A particular crop may reduce reserves of available nitrogen, phosphate and potash in equivalent proportions, or it may absorb relatively greater quantities of one particular nutrient. This effect of crop growth, unless subsequent adjustment be made by addition of artificial fertilisers to the soil, must sometimes modify the resistance of the following crop to certain root-infecting parasites (*see* above, p. 54). Thus VANTERPOOL (1930-40), for example, demonstrated that the browning root rot of cereals in Saskatchewan, due to *Pythium* spp., was worse after fallow than after a wheat crop; he attributed this unwelcome effect of fallow to an increase in the nitrogen/phosphate ratio of the soil, which apparently lowered the resistance of wheat plants to this disease.

*Chapter 10*

# CONTROL OF ROOT DISEASE IN FIELD CROPS: PLANT SANITATION

The problems to be discussed under this heading arise chiefly during and after harvest of a crop in which a soil-borne disease has been prevalent, since they concern the best method for treatment and disposal of infected seeds, propagating sets, and other crop residues. Infected seeds or propagating sets must be either eliminated or so treated that they do not carry infection into the next crop and perhaps onto "clean" land as well. Other infected residues, of no value for propagation, must be destroyed at once, if possible; if not, precautions should be taken to prevent their passive dispersal by the agencies of wind, water, man and his domestic animals. The gradual decline of a parasite when the land is occupied by non-susceptible crops has just been discussed; there remain for consideration those measures that can be taken to accelerate this "normal" disappearance.

**Preventing Dispersal of Parasite by Infected Seed:** — The prevention of disease transmission by infected seed or propagating sets is perhaps the most important part of crop sanitation; loss due to disease in a following crop, though considerable, may be negligible by comparison with the cumulative loss due to infection of clean land. The cereal smuts are the best known seed-transmitted diseases. In some of these, the spores are held mechanically, either adhering to the seed coat, as in bunt (*Tilletia tritici* and *T. levis*) of wheat, or enclosed within the glumes, as in covered smut (*Ustilago hordei*) of barley; these diseases can be controlled by seed treatment with a protective fungicide, such as the organic mercurial compounds now widely used for this purpose. In others, such as loose smut of wheat (*Ustilago tritici*) and of barley (*U. nuda*), the smut fungus is carried as a latent mycelial infection within the tissues of the seed, and so cannot be reached by surface disinfectants. The "modified hot-water treatment", invented by JENSEN (1888), is still used for control of these loose smut diseases of wheat and barley, but is not widely employed on account of the difficulties of operation, which involve skilled supervision, and also because the treatment is liable to reduce percentage germination of the seed. An ingenious application of this principle of control has been worked out by LUTHRA and SATTAR (1934) for Indian conditions (LUTHRA, 1941). The treatment is carried out in June or July; the infected seed is presoaked in water at indoor temperature for 4 hours from 8 a.m. to 12 noon, and is then taken out and exposed to the sun from 12 noon to 4 p.m. Complete control of loose smut has been obtained in this way, and the reduction in germination of the treated seed is negligible (not exceeding 2%).

The method is said to be applicable only to the hotter parts of the Punjab plains; maximum shade and sun temperatures at Lyallpur in June are stated to be 49° and 55°C. (120° and 131°F.), respectively. Further information concerning seed treatment may be found in the reviews of LEUKEL (1936), CUNNINGHAM (1935), and MARTIN (1940).

**Preventing Dispersal of Parasite by Infected Propagating Sets:** — The best known soil-borne diseases transmitted by vegetative propagation of the host plant are those of the potato. They include wart (*Synchytrium endobioticum*), scab (*Actinomyces scabies*), stem canker and tuber scurf (*Rhizoctonia solani*), and wilt (*Verticillium albo-atrum, Fusarium oxysporum* and *F. solani* var. *eumartii*). No effective method of tuber treatment for elimination of wart is in use, and the movement of seed tubers from an infected area has been controlled by quarantine legislation in many countries. Tuber treatment by steeping or dusting has been widely advocated for prevention of stem canker, black scurf and scab, but the value of such treatments for this purpose is often questionable. Both *R. solani* and *A. scabies* are widely distributed in most potato-growing soils; the planting of infected "seed" must often fail to increase either the amount of disease in the current season's crop, or the volume of inoculum of either parasite left behind in the soil after lifting of the crop. *R. solani* admittedly has a considerable power of movement through the soil (BLAIR, 1943); its mycelium probably grows not only from the seed or parent tuber along the sprouts, perhaps causing stem canker, but may also extend directly through the soil to the later-formed daughter tubers, there to cause the black scurf form of this disease.

*Actinomyces scabies,* on the other hand, appears to possess little or no power of free movement through the soil, as demonstrated by SANFORD (1933) in a masterly experimental analysis of the arguments for and against seed tuber treatment for control of scab. SANFORD'S experiments may be summarised as follows: (i) four tuber steeps, *viz.* hot formaldehyde, cold formaldehyde, mercuric chloride and a proprietary compound, failed to reduce incidence of scab on the crop in a field experiment, nor was scab increased by the use of planting sets almost covered with scab lesions, (ii) when sets were coated with a virulent agar culture of *A. scabies,* only a slight increase of scab occurred on the daughter tubers as a result of this, and then only on a few of the tubers that grew very close to the inoculated planting set, (iii) when planting sets were surrounded by a culture of *A. scabies* on sterilised soil, only that part of any daughter tuber which grew actually into the soil inoculum was covered by scab, (iv) in sterilised soil, *A. scabies* grew vigorously almost in contact with potato cores treated with the different protective steeps and dusts. SANFORD therefore

concluded that tuber treatments, whether or not they reduced the amount of *A. scabies* inoculum persisting in the soil from the original planting set, certainly failed to decrease the incidence of scab in the current season's crop.

An interesting study of the transmission of *Verticillium albo-atrum* to the tubers, and of the spread of this parasite under the growing crop, has been made by McKAY (1926), who showed that inspection of seed tubers was of little value as an aid to detection of infected ones; separation of tubers with discoloured stem ends, and discarding of stem ends in cut seed tubers alike failed to eliminate carry-over of infection in the seed tubers. McKAY therefore concluded that rogueing of the parent crop in the field was the only effective way of reducing "seed" transmission of this wilt disease to negligible proportions. Periodic rogueing of wilted plants (*i.e.* those showing above-ground symptoms), alone, was insufficient, since by the time such individuals had become obviously diseased, the neighbouring plants on either side of them in the row had usually contracted the infection as well. McKAY therefore recommended "three-plant rogueing", whereby the wilted plant was removed together with the two adjacent plants in the same row, at periodical crop inspections throughout the growing season. In one experiment, where the percentage of visibly wilted plants was 22, single-plant rogueing reduced the percentage of infected tubers to 8.4, and three-plant rogueing to 3.2. From the data obtained in these experiments, however, McKAY concluded that infected tubers could be eliminated from the crop as effectively by marking the plants for elimination, and digging separately at harvest, as by pulling them when first seen; even three-plant rogueing failed to reduce spread of the disease to the second plants away from the wilted one in the row.

**Destruction of Other Infected Crop Residues:** — One of the simplest and most effective methods for disposing of infected aerial parts of diseased cereals is to fire the straw after harvest, a procedure that has been followed for many years in Australia for control of the take-all disease (McALPINE, 1904; GRIFFITHS, 1933); this procedure also eliminates plant material infected by the flag smut organism, *Urocystis tritici* (McALPINE, 1910). In the past, Australian wheat has usually been harvested by the "stripper", which removes the heads alone, leaving the long straw standing; the straw never fails to burn well after the hot, dry summer, and the basal infected part of the stubble is usually completely destroyed. Although *O. graminis* continues to survive in the infected root and crown left behind in the soil, this source of infection is generally less massive, and therefore likely to disappear more quickly, than the infected base of the straw. Nevertheless, this practice of firing the straw is to be deprecated except when dealing with extensive infections, since the rapid depletion

of the soil humus is likely to lead to serious soil erosion in countries with a climate like that of Australia.

Extraction of infected crop residues from the soil, either by hand labour or by machine, is a measure deserving some consideration. No such expedient seems to have been tried out against any of the important soil-borne diseases due to fungi; in the Anglo-Egyptian Sudan, however, the carry-over of the leaf curl virus of cotton from one season to the next has apparently been prevented by hand-pulling (after harvest) of the plants, which are "yanked" out of the ground by an ingenious implement devised by MASSEY (1934). Treatment of the soil by fungicides might seem to be the obvious method for destroying infected crop residues, but this expedient is rarely economically sound for field crops, although soil sterilisation by heat or by chemicals has become a routine practice in intensive glasshouse culture (*see* chapter 15).

**Preventing Dispersal of Parasite by Other Agencies:** — *Dispersal by wind.* — Wind dispersal of fungus spores and infected plant debris is probably of less importance than was formerly supposed. Wind-borne fragments of infected wheat straw and dried grass haulm carrying *Ophiobolus graminis* were thought by MCALPINE (1904) to be reponsible for spread of the take-all disease in Australia, and SAMUEL (1924) has described an apparent instance of such dispersal; nevertheless, FELLOWS and FICKE (1939) tried experimentally to simulate such natural dispersal of infected soil by air and water in Kansas, and concluded that spread of *O. graminis* in this way must be slow and uncertain. Infection of roots by spores often fails to occur in the absence of a food-base (*see* above, p. 29), though provision of a food-base external to the fungus may be unnecessary in the event of a "mass-infection" by a number of spores simultaneously; the aggregate reserves of a sufficient number of spores presumably provide a food-base adequate to sustain the fungal invasion and establish infection in spite of host resistance. *Now wind-dispersal must eliminate opportunity for mass-infection by fungus spores.* The efficiency of spores in transmission of disease with the seed of many species of plant may be attributed in part to the occurrence of mass-infection; thus HEALD (1921) demonstrated a relationship between the spore-load of contaminated wheat seed and percentage of bunted heads in the resulting crop. Similarly, SHEN (1940) demonstrated that the percentage incidence and the severity of seedling blight due to *Fusarium culmorum* in wheat seedlings depended upon the spore-load of the seed.

The most convincing argument against wind as an important agent for dispersal of soil-borne parasites is the efficiency of crop rotation in controlling these parasites; although instances of failure

to achieve control of root disease by crop rotation are known (*see* above, p. 83), there is little evidence to suggest that such failures are at all frequently due to wind dispersal of the parasite. The best-authenticated example of air-borne contamination of soil is that afforded by bunt of wheat. Infection via the soil is especially important in the Pacific Northwest of the U. S. A., according to HEALD (1932), for the following reasons: Winter wheat in the Pacific Northwest is generally sown on summerfallow; crops mature earliest in the western or southwestern part of the area, and the "smut shower" released by threshing of these early-maturing crops is carried by the strong prevailing westerly winds over the summerfallows of the rest of the Pacific Northwest area. The summers are exceptionally dry with little or no rain in July and August to cause germination of the bunt spores that have fallen on the fallows; the autumn temperatures at and shortly after sowing time are favourable for infection of the winter wheat seedlings by the bunt fungus.

*Dispersal by water.* — The contamination of water supplies by the spores of parasitic fungi was investigated by BEWLEY and BUDDIN (1921), who found surface water such as that from ponds and brooks to be much more heavily contaminated than Company's water or that from deep artesian wells. CURZI (1927) found that *Phytophthora hydrophila,* causing root rot of chilli peppers in Italy, was spread by water; a single irrigation was said sometimes to result in the complete destruction of the crop. For the control of a similar disease (here attributed to *P. palmivora* var. *piperis*) of chillies in Batavia, MULLER (1936) recommended that a network of shallow trenches should be dug, with water pits at intervals to prevent the rain water running off over the surface. If infection occurred in one of the squares isolated by the trenches, the soil and diseased plants were to be watered with 1% solution of copper sulphate, and weeding temporarily discontinued. CRAWFORD (1934) has commented upon the spread by irrigation water of the *Fusarium annuum* wilt of the same crop in New Mexico. THUNG (1932, 1938) found *Phytophthora parasitica* var. *nicotianae,* the agent of black shank of tobacco in Java, to be carried by water from old tobacco fields, manure heaps, and curing barns. The movement of water in erosion and drainage from infected upper levels was considered by KING *et al.* (1943*b*) to result in the infection of lowlands and deltas by *Phymatotrichum omnivorum.* PELTIER (1937) repeatedly observed that when root rot occurred near the headwaters of a stream, it was usually distributed throughout the drainage basin, and that the incidence of the disease increased at the lower levels. HEWITT (1934) has made a similar observation on the spread of *Armillaria mellea.* The dispersal of sclerotia of *Sclerotinia sclerotiorum* by irrigation and flood water has been noted by BROWN and BUTLER (1936) in their study of lettuce "drop" in Arizona.

The importance of the passive spread of pathogenic fungi by water movement has thus been well established. Active spread by free-swimming zoospores of *Phycomycetes* and *Myxomycetes* is probably of negligible importance as far as actual dispersal is concerned. Thus HAENSELER (1926) found that zoospores of *Aphanomyces euteiches* were apparently incapable of migrating even half an inch in the soil, so that practically no spread of the disease in this way occurred in his experiments.

*Dispersal by cultivation operations and farm movements.* — Infected soil may be carried on the feet of farm labourers, and on those of draught animals and stock, as well as on implements. Such methods of spread have been cited, for example, by GIBBS (1931*a*) for the spores of *Plasmodiophora brassicae* on New Zealand farms, and by BROWN and BUTLER (1936) for the sclerotia of *Sclerotinia sclerotiorum* in Arizona.

*Dispersal by feeding diseased plant material to stock.* — The feeding of diseased roots to stock was shown by GIBBS (1931*b*) to constitute another mode of dispersal of *Plasmodiophora brassicae.* BROWN (1937) found *Sclerotinia sclerotiorum* to be spread in Arizona by feeding farm animals on infected lettuce refuse; on the other hand, sheep and other stock could be made to further the ends of plant sanitation by folding them on the infected plants after harvest, and quarantining them for four days, the maximum period for evacuation of living sclerotia. MCALPINE (1910) condemned the practice of feeding farm horses on wheat hay infected with flag smut (*Urocystis tritici*), and CLAYTON (1925) attributed the rapid spread of the disease in New South Wales to neglect of this advice, having shown that viable spores of *U. tritici* are voided in horse dung. In South Africa, VERWOERD (1929) succeeded in obtaining some 45% infection of test wheat seedlings not only with freshly voided horse dung, but also with the same dung when tested again the following season; sheep dung was also demonstrated to act as a vehicle for living spores of *U. tritici.*

*Dispersal in compost.* — The compost heap has often been indicted as a source of infection, whereby root-infecting fungi may be distributed over clean land. The high temperatures developing in a properly made compost heap must, however, be lethal to the mycelium and spores of many plant parasites. Thus GROOSHEVOY and LEVYKH (1940) reported that compost heaps prepared for tobacco seed-beds developed internal temperatures of 49°-63°C., which proved fatal both to the chlamydospores of *Thielaviopsis basicola* and to the pseudosclerotia of *Rhizoctonia* sp. Moreover, only a very small minority of the root-infecting fungi are sufficiently vigorous saprophytes to spread actively through a compost heap, in face of the competition of obligate saprophytes. An example of such a one has been given by

THOMPSON (1940), who declared that compost heaps in Malaya were sometimes heavily contaminated with *Sclerotium rolfsii,* and that the use of compost carrying this organism had been the cause of loss amongst ornamental plants in gardens.

**Accelerating "Natural" Disappearance of Parasite from the Soil:** — There remain for discussion those procedures whereby the normal rate of disappearance of a parasite from the soil under fallow or a non-susceptible crop can be accelerated by the farmer. Some field crop plants, for instance, do not die after flowering and fruiting, with the result that a root disease fungus may continue to survive and even to spread on the still living roots after harvest. Thus TAUBENHAUS and EZEKIEL (1930*b*) demonstrated the survival and spread of *Phymatotrichum omnivorum* throughout the winter on living cotton roots, long after the tops of the plants had been killed by frost. REA (1933) reported that winter cultivations reduced the number of live, over-wintering cotton roots, but that reduction in this source of infection alone failed to reduce appreciably the incidence of root rot in the following season.

In general, the period of survival of a root-infecting fungus in the interval between susceptible host crops is likely to be most brief under those conditions most favourable for its vegetative activity, and therefore least favourable for dormancy. Under such conditions, resting spores and sclerotia are likely to germinate more freely, and mycelium in infected tissues more quickly to exhaust the food reserves of the substrate. Thus BREMER (1924) considered that, in the absence of host plants, *Plasmodiophora brassicae* was likely to survive for longest in alkaline soils, which inhibited spore germination; in alkaline soils, moreover, the spores were most resistant to the lethal action of mercuric chloride or high temperatures. GARRETT (1938*b*) and FELLOWS (1941) concluded that the period of survival of *Ophiobolus graminis* in infected host tissues was shortest in warm, well aerated and moist soils, *i.e.* under just those conditions optimum for vegetative activity.

Methods most likely to be of use in hastening the disappearance of a root-infecting fungus from the soil in the absence of host plants may be listed under three heads: (i) cultivation, (ii) organic manuring, (iii) use of selected rotation crops or catch crops. Several experiments on the value of cultivation for eradication of *Phymatotrichum omnivorum* have been carried out; results obtained by REA (1933) and RATLIFFE (1934) were not encouraging, but STREETS (1937) and REA (1939) have since quoted more promising results, especially from deep subsoiling. STREETS drew attention to survival of *P. omnivorum* below cultivation depths as one of the reasons for the limited success of cultivation in eradicating the fungus, and REA connected the greater success of modern trials of deep tillage with the more

powerful implements employed. MITCHELL *et al.* (1941) obtained encouraging results from rotary tillage early in the autumn after cotton harvest, as compared with the usual late autumn ploughing; in the following August, sclerotia were abundant between the 6 and 12 inch soil levels of the ploughed plot, but absent in the upper 12 inches of soil in all the rotary-tilled plots. This reduction in sclerotial population was associated with reduction in the incidence of root rot in the cotton crop; incorporation of farmyard manure or sorghum fodder with the soil by means of the rotary cultivator still further reduced losses from root rot (*see* above, p. 80).

MITCHELL *et al.*, and CLARK (1942), by demonstrating that disappearance of the sclerotia of *P. omnivorum* was greatly stimulated by the addition of organic material to the soil, helped to explain the control of cotton root rot through organic manuring reported by KING *et al.* (1934*a*). KING'S success with this method in Arizona, as compared with its failure in Texas (REA, 1939), may be attributed in part to the difference between irrigation farming in Arizona and dry-land farming in Texas, and in part to the special methods for timing and placement of the application recommended by KING (1937): "The method consists of applications of various organic materials in deep furrows during the fall and winter, and in planting the cotton over the buried material. The furrows for the manure should be from 10-14 inches deep, so that the buried material will not interfere with the preparation of a seed-bed. . . . It has been found that as much as 20 tons of horse or cow manure from corrals or open stalls per acre may be used without injury to the cotton crop. However, 15 tons per acre probably would be adequate for most conditions. Where green material such as freshly cut alfalfa, clover, field peas, vetch or mustard is available, 30 tons per acre may be used if furrows are made deep enough so that the material may be covered with 5 or 6 inches of soil. . . . Irrigation water should be applied immediately (*i.e.* after covering) so as to compact the soil and encourage the activity of organisms for decomposition. If possible, the organic material should be applied, covered, and irrigated at least a month before planting time, and a second irrigation should be made before planting to ensure adequate moisture for germination of the cotton seed."

Evidence for the view that rotation crops non-susceptible to infection by a particular parasite may yet affect the period of its survival has already been discussed (p. 88). Germination of the resting spores and sclerotia of root-infecting fungi may sometimes be stimulated by contact with the roots of plants other than their host plants (NOBLE, 1924); search for such plants seems to offer a promising line of investigation.

*Chapter 11*

# CONTROL OF ROOT DISEASE IN FIELD CROPS: DISEASE CONTROL UNDER THE GROWING CROP

In chapters 4-6, variation in the incidence of soil-borne diseases was analysed as far as possible, and related to variation in the component factors of the soil environment, *viz.* temperature, moisture content, texture, reaction, organic content, and concentration of plant nutrients. This chapter will be concerned with the practical application of such information; control measures will be discussed under the following heads: —

(i) mechanical methods
(ii) amelioration of soil temperature
(iii) management of soil moisture content and aeration, and variation in depth of planting
(iv) modification of soil reaction
(v) use of organic supplements
(vi) application of artificial fertilisers.

**Mechanical Methods:** — Mechanical methods have attained their greatest development as measures for control of root disease in plantation crops, and have thus far found few applications in field crop practice. Some use has been made of mechanical barriers for delimiting the spread of *Phymatotrichum omnivorum* into clean areas, by means of trenches filled with mixtures of soil and heavy oils, sulphur, ammonia, carbolic acid or salt, both in Texas (TAUBENHAUS and EZEKIEL, 1931) and in Arizona (STREETS, 1937). Quite a different type of barrier was developed in Texas by TAUBENHAUS and EZEKIEL (1931), who found that 4-12 rows of sorghum stopped the spread of *P. omnivorum;* the roots of the sorghum prevented those of the cotton on either side of the barrier from making contact with one another.

A direct mechanical effect of inter-row cultivation of potatoes in breaking root contacts between adjacent rows of the crop was suggested by MCKAY (1926) as the reason for failure of *Verticillium albo-atrum* to spread from one row to another during the growing season, though it spread freely along the rows, as far as the second or third plant away from the one first showing wilt symptoms. MCKAY suggested that the practice of planting in check rows, so as to permit of cultivation in either direction, would probably prevent the spread of this disease, and that this procedure might eliminate the necessity for "three-plant rogueing" in crops intended for "seed" production.

**Amelioration of Soil Temperature:** — Control of soil temperature cannot be directly secured in the field as it can in the glasshouse, but the range of temperature under which the crop develops can be

varied to some extent by alteration in planting date. Information concerning the optimum temperature for the development of particular soil-borne diseases and the safest time for planting of the host crops concerned is given above in Chapter 4.

An interesting new method of root disease control, apparently achieved through reduction of soil temperature, has been independently reported by VASUDEVA and ASHRAF (1939) in India, and by HANSFORD (1940) in Uganda. VASUDEVA and ASHRAF, investigating the Indian root rot of cotton, which is caused by *Rhizoctonia solani* and *R. bataticola,* found the optimum temperature for disease development in Wisconsin-type soil temperature tanks to be rather high; seedling mortality due to *R. solani* was highest at 35°C., and that due to *R. bataticola* at 39°C. In a mixed crop of cotton and sorghum, the deaths of cotton plants from root rot were significantly fewer than those in cotton alone. VASUDEVA and ASHRAF attributed this reduced mortality to the shading effect of the sorghum in lowering soil temperature; the humidity of the air was higher in the mixed crop, but no consistent increase or decrease in soil moisture content was found. VASUDEVA (1941) later reported further experiments confirming and amplifying these results. Whereas sorghum tended to reduce the yield of cotton in mixed cropping even on heavily infected land, the growth of "moth" (*Phaseolus aconitifolius*) in between the cotton rows not only reduced the mortality in the cotton from more than 50% in the pure stand to a negligible percentage in the mixed crop, but also significantly increased the yield of seed cotton. Soil and air temperatures were lower in the mixed crop, and humidity was higher, than in the pure cotton. In a mixed crop of cotton and "swank" (*Panicum colonum*), in which the "swank" got a poor start, soil and air temperatures were no lower than those in the pure cotton plots; nevertheless, mortality due to root rot was significantly lower in the mixed crop than in the pure stand of cotton. VASUDEVA therefore concluded: "Temperature may be an important factor, but it is likely that some other factor also comes into play which helps in reducing the incidence of the disease, as in the case of *swank* where the temperature was not materially affected in the mixed crop but the incidence of the disease was reduced." One such "other factor" that is likely to operate in reducing mortality due to disease in a mixed crop (where the plant used for inter-cropping is immune to infection) is the interruption of root contacts between susceptible plants by the roots of immune plants.

HANSFORD (1940) reported a similar result obtained by J. D. JAMESON in field experiments on the wilt disease of cotton (more than 90% of which was attributed to *Verticillium dahliae,* and the remainder to strains of the Elegans section of the genus *Fusarium*), carried out at Bukulasa Station in Uganda. The incidence of wilt

was diminished both by reducing the distance between the cotton rows, and by interplanting with groundnuts or beans. The effect was attributed to lowering of the soil temperature, which was stated to vary at Bukulasa from 76°-86°F. (24°-30°C.). In the Eastern Province of Uganda, on the other hand, where mean soil temperatures were higher than at Bukulasa, the wilt disease tended to be more prevalent under shade.

**Management of Soil Moisture Content and Aeration, and Variation in Depth of Planting:** — The incidence of a root disease favoured by high soil moisture content can often be reduced by attention to field drainage. A reduction in moisture content of the soil around the roots and base of the plant, with beneficial results in diminishing the incidence of a soil-borne disease, can sometimes be secured by planting crops "on the ridge", as advocated by Coons *et al.* (1941) for control of black leg (species of *Pythium, Rhizoctonia,* and *Aphanomyces*) in sugar-beets, and by Garcia (1933) for control of wilt (*Fusarium annuum*) in chilli pepper.

Crops grown under irrigation form an exception to the general rule that soil moisture content under field crops cannot be varied except by indirect methods. More diseases, unfortunately, seem to be favoured by high soil moisture content than are favoured by low soil moisture content, so that the grower more often reduces incidence of disease by abstention rather than by exercise of his advantage over nature. A notable exception is offered by the cereal smuts, the control of which under irrigation has recently been investigated with conspicuous success by Jones and Seif-el-Nasr (1940). As a brief account of cereal cultivation under irrigation in Egypt is necessary for comprehension of these results, that given by Jones and Seif-el-Nasr is quoted: "Wheat and barley under perennial irrigation in Egypt are either planted by the *herati* method of broadcasting seed on moist land and ploughing it in, or else by the *afir* method of broadcasting on dry land, harrowing in the seed with a baulk of wood and irrigating. . . . Examination of pairs of wheat fields in which all other factors were said to be the same, but in which both methods of planting were used, showed that *herati*-sown plots consistently gave more flag smut than *afir*-sown plots. Later experiments showed that there was two to three times more flag smut in *herati*-sown plots, and similar tests with barley proved that the *herati* plots were six times more heavily attacked by covered smut than the *afir* plots, thus explaining satisfactorily the result. Later still, it was found that bunt of wheat and grain smut of millet and broom corn were almost equally sensitive to difference in method of planting. . . . The most obvious difference between the *herati* and *afir* methods of planting is in soil moisture, the *herati* plots being only moist enough for good ploughing, while *afir*

plots, being irrigated immediately after sowing, are wet. A second difference lies in the depth at which the seed is planted. In *herati* plots the seed is covered with a plough set at 12-15 cm. depth, so that the seed is buried at any depth between the surface and the plough sole: seeds which happen to be left near the surface fail to germinate owing to lack of moisture, while the most deeply buried seeds germinate poorly, so that the average depth of effective planting is about 8 cm. In the *afiir* plots the seeds broadcast on the surface are covered by harrowing with a wooden baulk while the land is dry, and are thus buried only about 4 cm. deep before they are irrigated."

JONES and SEIF-EL-NASR proceeded to determine the reasons for this difference in incidence of cereal smuts under the *afir* and *herati* methods of sowing, by comparing the incidence of smut in plots sown under moist and wet conditions, and at 4 depths of planting, *viz.* 0.5, 4, 8 and 12 cm. The moisture content of the "moist" soil corresponded to that of the *herati* plots, and the moisture content of the "wet" soil to that of the *afir* plots. Experiments were carried out with the diseases caused by four smut fungi, *viz.* flag smut (*Urocystis tritici*) and bunt (*Tilletia levis*) of wheat, covered smut (*Ustilago hordei*) of barley, and grain smut (*Spacelotheca sorghi*) of millet and broom corn. The effect of higher moisture in decreasing the incidence of smut was consistent throughout the experiments, all diseases behaving in the same way. The effect of depth of planting was still more pronounced, and almost as consistent; the percentage of smut increased with depth of sowing, presumably (as JONES and SEIF-EL-NASR suggested) because the period during which the host was susceptible to infection was thereby prolonged. The only exceptions to this rule were afforded by the incidence of bunt of wheat at 12 cm. depth in wet soil, which was less than that at 8 cm. depth, and by the incidence of grain smut of broom corn, which decreased as depth of sowing increased from 4 through 8 to 12 cm. In explanation of these exceptions, JONES and SEIF-EL-NASR suggested that under the conditions of deep planting in wet soils the smut fungi tended to become destructively parasitic, and to kill the infected seedling below ground; the *apparent* percentage of infected plants, as determined by counts at harvest, would in this way be diminished. Nevertheless, infection by all the smut fungi concerned in these experiments is favoured by good soil aeration, as shown by the consistently higher incidence of infection in the moist as compared with the wet soils; it seems possible, therefore, that in the wet and less well aerated soil the advantage offered to the fungus by deeper sowing, through prolongation of the susceptible period of the cereal seedling, might be more than offset by the disadvantage to it of further reduction in oxygen supply.

These exceptions, however, are of minor practical interest; the extensive data collected by JONES and SEIF-EL-NASR in these experi-

ments indicate that the advantage of the *afir* over the *herati* method of sowing in smut control is to be attributed both to the shallower sowing and to higher soil moisture content during the pre-emergence period. As JONES and SEIF-EL-NASR have pointed out, the logical extension of the *afir* method of planting for better control of smut is "mud sowing" at zero depth and maximum soil moisture; this could be practised on land prepared either as for *herati* or as for *afir* planting. Results obtained by JONES and SEIF-EL-NASR in two experiments to compare the effect of different methods of planting on the incidence of flag smut in wheat are given in Table 14.

TABLE 14. *Effect of planting method on incidence of flag smut (Urocystis tritici) in wheat:—*

| PLANTING METHOD | CULTURAL OPERATIONS | APPROX. RESULTANT DEPTH OF SOWING (cm.) | SOIL CONDITION AND PERCENTAGE MOISTURE* AT SOWING DEPTH AND AT SOWING TIME | FLAG SMUT (%) Exp. 1 | FLAG SMUT (%) Exp. 2 |
|---|---|---|---|---|---|
| *Herati* | Seed broadcast on moist soil and ploughed in | 8 | Moist, 25% | 8.1 | 8.6 |
| *Afir* (usual) | Seed broadcast on dry soil, harrowed in with a baulk and irrigated | 4 | Dry then wet, 8 then 32% | — | 3.2 |
| *Afir* (modified) | Seed broadcast on dry soil, covered by raking, and irrigated | 2.5 | Dry then wet, 8 then 32% | 2.4 | — |
| Mud sowing (method 1) | Moist soil ploughed and flooded: seed broadcast on surface 1 hr. later | Nil | Sodden, 41% | 0.2 | — |
| Mud sowing (method 2) | Dry soil flooded: seed broadcast on surface 1 hr. later | Nil | Sodden, 41% | — | 0.08 |

* Approximate mean percentages of weight of the moist soil.

Concerning the very satisfactory control of flag smut obtained through mud sowing, JONES and SEIF-EL-NASR declared that method 1 appeared to promise increased yields and better quality of grain, apart from the control of smut, and that there was no sign of increased tendency towards lodging, as might perhaps have been expected. This method should be particularly valuable for control of flag smut in Egypt, where infection, as in other countries, is soil-borne as well as seed-borne (JONES and SEIF-EL-NASR, 1939).

The method of preparing the seed-bed has also a most important influence upon the occurrence of the take-all (*Ophiobolus graminis*) disease of cereals, which is encouraged by loose, badly compacted soils; control must therefore be sought through preparation of a particularly firm seed-bed for wheat. Such a seed-bed is best secured through early preparation and sufficient working at the correct times,

so that the underlayers of the soil become consolidated by the joint action of implements and the weather; the consolidating effect of rain has been particularly stressed. A poor seed-bed, on the other hand, results from too late and hasty a preparation, when a tilth has to be "forced" by the use of implements, instead of maturing with time and action of the weather. In the same way, the ploughing-in of long straw or dry grass, which opens up the soil, or dry ploughing and working of the land, which produces a similar effect, has been found to encourage the disease.

**Modification of Soil Reaction:** — Control of the clubroot disease of crucifers by application of lime is too well established to require detailed comment. For this purpose, the oxide and hydroxide of lime are much more effective than the carbonate, with which disappointing results have frequently been reported. Thorough incorporation of the lime with the soil down to ploughing depth is obviously essential for complete control of this disease; for this reason, the lime is best applied a year or so before the cruciferous crop is sown. The widespread adoption of lime for control of clubroot owes much to the fact that liming of acid soils greatly increases the yield, and often the quality, of the majority of field crops, apart from control of clubroot.

In contrast to the general employment of lime against clubroot, the adoption of sulphur as a soil-acidifying agent for control of such diseases as Texas root rot of cotton, scab of potatoes, take-all of cereals, and black root rot of tobacco has scarcely left the experimental stage. The acidification of neutral soils by addition of sulphur is likely to lower the yield of many crops; on highly alkaline soils, such as those of arid regions (and especially soils under irrigation), the application of sulphur may improve crop growth by decreasing soil alkalinity, but the cost of the very heavy applications of sulphur necessary to produce this effect is likely to be too high for commercial farming. Although soil acidification with sulphur cannot as yet be recommended as a practical measure for control of these diseases, useful cautionary advice can be given to farmers on slightly acid or neutral soils, *viz.* to be careful in the use of lime, and preferably to leave the soil with a slight lime requirement.

**Use of Organic Supplements:** — The control of cotton root rot in Arizona through application of organic manures to the soil has already been discussed (pp. 53, 79, and 97). The control of potato scab by green manuring is sometimes extremely successful, especially in private gardens and on small-holdings where grass cuttings, etc., can be incorporated with the soil in amounts that would be quite impracticable in the field. In the field, indeed, green manuring is by no means always successful in controlling scab, as SANFORD (1939)

has observed. In pot experiments demonstrating the control of scab and other diseases by organic manuring, the green manure has usually been dried and ground, so that incorporation with the soil has been very uniform; in small plot experiments, the green manure has usually been chopped up with a chaff cutter, for the same reason. When green manuring is practised in the field, however, the organic material is usually ploughed into the soil in swathes, so that the resulting mixture of soil and organic material is far from homogeneous; a more uniform and thorough incorporation can be achieved by means of the rotary cultivator. For the cotton crop, KING (1937) has ingeniously surmounted this difficulty by planting the cotton rows right on top of the trenches in which the fresh organic material has been buried.

Even the most sanguine investigator should not be surprised, therefore, if the history of his pot experiments fails to repeat itself in the field. The slow progress made by such comparatively new methods as organic manuring for control of root disease in field crops is not surprising; wherever possible, the farmer achieves a satisfactory degree of control through crop rotation, modification of cultural practice, and application of artificial fertilisers.

**Application of Artificial Fertilisers:** — The effect of the concentration of plant nutrients in controlling or aggravating incidence of soil-borne diseases has already been discussed in chapter 6 (p. 54 *et seq.*), and little more need be added here. Recommendations to apply artificial fertilisers to assist in root disease control are more likely to be adopted by farmers than most other suggestions made by plant pathologists, because an increase in crop yield can usually be guaranteed even in the absence of disease.

*Chapter 12*

# CONTROL OF ROOT DISEASE IN PLANTATION CROPS: ON VIRGIN AREAS

Any discussion of root disease in plantations must be concerned chiefly with the diseases of tropical crops; root disease is of greater importance in tropical plantations than in those elsewhere. The root diseases of rubber have received the greatest attention, followed by those of tea and cacao; the banana suffers from only one root disease of any importance, *viz.* Panama disease, but that one disease has caused, and is continuing to cause, enormous losses. An outstanding contribution to our knowledge of the subject has been made by the Rubber Research Institute of Malaya, and the principles of root disease control that they have formulated are of general application to plantation crops. No apology need be made, therefore, for concentrating attention upon the root diseases of tropical crops in general, and upon those of rubber in particular.

Tropical plantations are generally established, in the first instance, upon the site of virgin jungle, which has to be cleared to a greater or less extent before the crop can be planted; various root disease fungi occur throughout the root network of the original jungle, and some of these find congenial hosts in the plants of the young crop. The simplest solution of the root disease problem is to place the cleared area under annual field crops, which are not susceptible to tree root diseases, for a period of years, but this method has never found favour with plantation owners, on account of the long delay involved. Thus NAPPER (1934) commented upon the absence of root disease in rubber planted on land cropped for long periods after clearing with sugar-cane, rice, etc., and also upon the slight amount of root disease to be found on the average small-holding. A specific example has been cited by SHARPLES (1936): "Tapioca was extensively cultivated before the rubber era in certain districts in Malacca and Kedah. These old tapioca areas were allowed to become derelict, in some cases for many years, after being abandoned, and they became covered with a heavy, coarse growth of 'lallang' grass (*Imperata arundinacea* Cyrillo). Many of these areas were later planted up with rubber, and usually there were few signs of jungle stumps or timber remaining when the work was put in hand. Some of the estates in the Malacca district are large properties, and practically no reports of root disease have ever emanated from those opened up on 'lallang' land."

Root diseases may develop from the stumps (*i.e.* stumps + roots) of the original jungle trees, if these are left behind after felling and clearing. Two additional sources of root disease are provided by the stumps of trees that have to be thinned out because the original planta-

tion was too closely planted, and by the stumps of shade trees that are felled when they have fulfilled their purpose of providing shade for the developing plantation crop. On the subject of thinning out in rubber plantations, PETCH (1921) remarks: "Close planting with the intention of thinning out in later years, was never widely adopted; in the majority of cases estates were planted up at the distances it was considered the trees would remain permanently. It needed, however, only the efflux of time to demonstrate the truth of the prophecies of mycologists who contended that *Hevea* could not possibly exist in a healthy condition when planted two hundred to the acre; and the necessity for thinning out all the earlier-planted Rubber is universally admitted."

**Early Methods of Root Disease Control:** — A good account of the classical methods for root disease control has been given by PETCH (1921). In the first place, clean clearing of the original jungle was favoured wherever practicable, in order to remove all possible sources of infection. Although PETCH admitted the probable presence of infected roots in the jungle stand, he laid much greater emphasis upon another source of inoculum, provided by air-borne spore infection of the cut surfaces of the stumps after felling. He supposed that once spore infection of the cut surface had been established, the parasite grew down into the roots of the stump, thence eventually to emerge and infect the roots of the young plantation crop, either through root contact or, with some fungi (*e.g. Fomes lignosus*), by direct spread through the soil. Diseases considered especially likely to spread in this way were white root disease (*Fomes lignosus*), brown root disease (*Fomes noxius*), and charcoal root rot (*Ustulina zonata*), but other root diseases, such as red root disease (*Ganoderma pseudoferreum*), unknown to PETCH in Ceylon, were not excluded from the same category. This hypothesis was held to explain not only the development of root disease from the stumps of the felled jungle, but also that following the thinning out of shade trees. It is a remarkable fact that no experiments to prove this hypothesis ever seem to have been reported, although the technical difficulties in the way of protecting the cut surface of the felled stump from spore infection would scarcely seem to have been insuperable; in the meantime the hypothesis held undisputed sway for many years, and was acted upon in practice, either by extraction of the felled stumps, or by cutting them off below ground level and covering with soil (GADD, 1936*b*). Indeed, the discrediting of PETCH's hypothesis has been brought about not by any direct experimental assault, but rather through the gradual accumulation of circumstantial evidence in conflict with the hypothesis, and finally through the establishment by experiment of an alternative explanation (*see* below, p. 112).

For the treatment of definite patches of root disease, PETCH recommended the removal of all dead trees, decaying stumps and buried timber in the affected patch, the application of lime to the soil, and the isolation of the area by means of a deep trench. In removing the dead trees, the laterals had to be followed up and dug out; the affected patch had then to be forked over, and all pieces of dead wood collected and burned. The direction to apply lime was apparently based on the assumption that "the majority of fungi prefer an acid medium", an assertion even less valid than most generalisations. This assumption was shown by BRYCE (1922) not to hold for *Fomes lignosus,* the most important cause of rubber root disease in Ceylon, since when the application of lime has no longer been advised. The last part of the treatment lay in the digging of an isolation trench, which PETCH declared should enclose not only the diseased tree, but also a complete ring of surrounding, apparently healthy trees. He recommended a depth of 2 feet, but the depth had to be sufficient to ensure the severing of all lateral roots, so that a depth of 3 feet might sometimes be necessary.

The method of trenching to stop the spread of a root disease is an old established one; TUNSTALL (1940) remarks: "More than fifty years ago the foresters in Europe sought to prevent root disease spreading by encircling the diseased trees with shallow trenches. This method was adopted in the case of rubber, tea and coffee." PETCH (1923) evidently viewed the isolation trench as designed primarily to prevent the spread of free mycelium through the soil, and only secondarily to prevent spread of disease by root contact, as shown by the following quotations: "*Ustulina** usually attacks tea by spreading to its roots from the roots of decaying stumps. The fungus does not spread free through the soil, but only passes from the roots of the stump to those of the tea bush when the two are in contact. Consequently trenching might possibly be dispensed with in the case of this disease, but it is better to err on the safe side and to trench. . . . As *Armillaria mellea* produces thick black cords of mycelium (rhizomorphs), which spread freely through the soil, it is essential that the diseased patches should be isolated by trenching. . . . Since the mycelium of *Fomes lignosus* spreads freely underground, affected patches must be isolated by a trench." PETCH (1921) laid great emphasis on the free mycelial spread of *F. lignosus* through the soil, concerning which he remarks elsewhere: "The majority of fungi only advance within dead wood, but the strands of *Fomes lignosus* can travel for a few feet at least through the soil, unattached to any root or dead wood, except, of course, at their starting point. It is always attached to its base, *i.e.* the stump on which it originated, and it must derive its food from that source until it meets with other dead wood, or a living plant

* *Ustulina zonata.*

which it can attack. . . . Clear instances of the spread of the mycelium through the soil are not uncommonly met with on estates. In badly-infested areas its presence is often manifested by the appearance of the fructifications on banks by roadsides, or the sides of drains, where no roots or timber is to be seen. In some of these cases the mycelium follows small Rubber roots almost to the surface of the soil, but in others there is no root or wood to be found immediately behind the fructification. In other cases, it is often found running on the under surface of large stones, and in these instances it is readily seen, as a rule, that it is not following a root." The accuracy of PETCH's field observations has not been questioned by later investigators, though a different interpretation is now put upon them; in the instance quoted above, PETCH failed to discriminate between the spread of the fungus and that of the disease (*see* above, p. 26).

The classical view of the behaviour of these tropical root disease fungi, as presented by PETCH, may be summarised as follows: Root disease fungi present on the roots of the original jungle trees persisted on the roots of the stumps after felling; a more dangerous and wide-spread source of inoculum, however, was furnished by air-borne spores of the fungi, alighting on the cut surfaces of the stumps. From the crown, the fungi were assumed to spread down into the roots of the stumps, whence they infected the roots of the young plantation crop either by root contact, or, with *Fomes lignosus, Poria hypolateritia,* and *Armillaria mellea,* by free spread of the mycelium through the soil.

**Napper's Method of Root Disease Control:** — The classical theory of root disease control was undermined by the observations of NAPPER (1932-34), upon whose researches at the Rubber Research Institute of Malaya modern views of the biology and control of rubber root disease fungi are based. In the first place, NAPPER considered that all the root disease inoculum that gave trouble in the young plantation crop was present on the roots of the original jungle, and that spore infection of the felled stumps was of subordinate importance, if, indeed, it occurred at all. Thus NAPPER (1934) writes: "Being so advantageously equipped for life under forest conditions the root parasites have become generally distributed throughout the jungle. Since, however, they are normal members of the jungle association they do no spectacular destruction amongst the jungle trees, but here and there, like any other species, they become locally dominant, each particular parasite forming its own pattern of root disease patches scattered throughout the jungle stand. While the jungle is growing undisturbed, these patterns are perpetually changing in shape and position, but the total incidence of infection remains constant, and the loss of stand never becomes serious." Whereas PETCH had

stressed the difference between those fungi that spread as mycelium through the soil, such as *Fomes lignosus,* and those that spread by root contact, such as *Fomes noxius,* NAPPER, on the other hand, stressed the essential similarity in behaviour of the three important fungi infecting rubber roots in Malaya, *viz. F. lignosus, F. noxius,* and *Ganoderma pseudoferreum.* In NAPPER'S view, all three fungi had developed the subterranean organ of propagation — the rhizomorph — at the expense of the aerial organ, the fructification. Secondly, NAPPER'S field observations indicated that the importance of free mycelial spread through the soil by *Fomes lignosus* had been unduly emphasised, and that rhizomorphs could not grow (except under special conditions, and for short distances only) directly through the soil, but required as a vehicle a chain of solid surfaces, preferably those of living host roots. It was true that rhizomorphs might be found covering the underside of stones and boulders, and growing on dead roots, but they were unable to obtain nourishment from any substrate other than living host roots; the rhizomorphs could not, apparently, invade tissues already colonised by other organisms. NAPPER stressed this effect of microbiological competition in curtailing the spread of the root parasites, whether on the exposed wood surfaces of cut stumps, or on dead roots already occupied by other micro-organisms.

From the results of certain experiments originally set up by J. R. WEIR at the Rubber Research Institute of Malaya, on "clean clearing" *versus* no clearing in preparation of a jungle site for rubber, NAPPER derived certain important conclusions as to the behaviour of rhizomorphs, which were to form the basis of a new and outstandingly successful method for root disease control. The results of this experiment are given in Table 15.

TABLE 15. *Percentage infection by Fomes lignosus of young rubber planted on jungle site:* —

| | CLEARED | UNCLEARED | SECONDARY JUNGLE (BELUKAR) |
|---|---|---|---|
| Block 1.................. | 29.4 | 18.6 | — |
| Block 2.................. | 20.3 | 9.2 | — |
| Block 3.................. | — | — | 1.7 |

Two and a half years after planting, incidence of infection amongst the young rubber was lower where no clearing had been carried out than on the clean-cleared area; it was lowest where secondary jungle ("belukar") had been allowed to grow up as a natural cover. These results were in direct contradiction to the postulate of the classical theory that the amount of disease in the young plantation crop varied

directly as the amount of actual and potential inoculum left in the soil after clearing, and were explained by NAPPER as follows: —

(i) If "absolute" clean clearing is carried out and even the smallest pieces of buried timber are removed from the soil, *e.g.* by sieving, no actual or potential source of inoculum will be left, and a healthy young plantation will result.

(ii) Under "ordinary" clean clearing, as practised on commercial estates, a small amount of generally distributed timber is left in the soil. Now rhizomorph production does not start until the food material in an infected root section has been almost exhausted by the fungus (*see* above, p. 29) ; rhizomorph production therefore starts the soonest in the smallest pieces of infected root. It is precisely these small pieces of infected root that are left behind in the soil after "ordinary" clean clearing.

(iii) The larger pieces of infected material must therefore be considered relatively harmless to the young plantation crop, as they will not arrive at the stage of rhizomorph production for some time; they are not merely harmless, however, but are actually beneficial, as they represent solid surfaces upon which the growth energy of the rhizomorphs must be expended. The greater the area of solid surfaces, or obstacles, to be covered, the slower will be the advance of the rhizomorphs from their source, with the result that some of them may never achieve infection of the roots of the plantation crop.

Upon this last point, NAPPER (1932*a*) comments: "If the above reasoning is sound, then there is no difficulty in explaining why the presence of a cover crop, even of a woody plant such as *Crotalaria,* which is known to be parasitised by the fungus, tends to reduce the incidence of *Fomes lignosus* upon the rubber trees among which it is planted. . . . There is probably very much more mycelium in the soil under a heavy cover crop than under clean weeded conditions, but this is discounted as indicating the probability of a higher incidence of attack upon the rubber trees interplanted with a cover because of the larger amount of material in the soil other than the roots of rubber trees upon which the mycelium can feed." NAPPER's conclusions concerning the effect of a cover upon incidence of infection in the young plantation crop have been confirmed by CRONSHEY and BARCLAY (1939) in a well replicated replanting experiment of modern design (*see* below, p. 126).

An objection to the policy of planting on the uncleared site was anticipated by NAPPER (1932*a*) in the following words: "Although methods of planting under uncleared conditions, or conditions of secondary jungle, may greatly reduce the loss of stand through root disease during the early years of the clearing, the effect may be one of delayed action only. It has been deduced above that the probability of attack upon the crop plant is greatest when other rottable

material in the soil is nearly exhausted, and it may be that, in an estate which was planted under uncleared conditions, or under conditions of secondary jungle, the disease will attack the crop plant in an epidemic fashion in later years when the jungle timber in the soil becomes exhausted, or when the belukar (or other cover crop) is shaded out by the rubber. . . .Evidence suggests that as the rubber tree grows older it becomes more resistant to the attacks of *Fomes lignosus* on its roots, and further, that the culture of *Fomes lignosus* in the soil of a new clearing stales after a time and is not subsequently so active as during the first few years after clearing. This evidence is based on the observation frequently made that the incidence of the disease in a new clearing tends to rise to a maximum during the period between the second and the fourth years after burning off, and then to drop to a comparatively low figure." Even where few or no control measures against root disease are carried out, *Fomes lignosus* is typically the root disease fungus of young rubber plantations, up to ten years of age, whereas *Ganoderma pseudoferreum* is the root disease fungus characteristic of mature plantations. SHARPLES (1936) explained this by reference to the differences in rhizomorph behaviour of these two fungi. The rhizomorphs of *F. lignosus* grow very rapidly, but soon exhaust their food-bases, whereas those of *G. pseudoferreum* grow much more slowly, and exhaust their food-bases only after a much longer interval.

As a result of these discoveries NAPPER (1932*b*, 1938*b*) worked out a new method for dealing with root diseases, which is applicable not only to the disease caused by *F. lignosus,* but also to those caused by *Ganoderma pseudoferreum* and *F. noxius* as well; the method, although primarily designed for young plantations established on jungle sites, can be modified to suit the requirements of replanted areas. The ground, after felling and burning of the jungle, is cleared of the larger stumps, but the young rubber trees are themselves employed for the discovery of residual sources of infection, as follows: Every four to six months, a pest gang of trained labourers makes a tree-to-tree inspection of the whole plantation, in the course of which the upper tap root and laterals of every young tree are examined for rhizomorphs of the root disease fungi. The length of tap root that must be exposed varies from 2 inches at one year after planting to 9 inches at four years, if the soil is a deep one, but the depth of inspection must in any case be sufficient to uncover the undersides of the surface laterals. If rhizomorphs of a root disease fungus are found, the root system is opened up further until the whole extent of the invading mycelium has been exposed, and the source of infection discovered. The source of infection is then removed (and destroyed) and the roots of the jungle stumps are followed up systematically in every direction until all infected material has been disclosed and re-

moved. The root system of the young rubber tree is then pruned of all root sections that have already been penetrated by the parasite. The method depends for much of its success upon the fact that the rhizomorphs of *F. lignosus,* the most common cause of root disease in young Malayan rubber plantations, extend for 5-15 feet ahead of the infected part of the root. The roots carrying such superficial or epiphytic mycelium can be adequately treated simply by pulling away the larger rhizomorphic strands, and then washing the root surface with a 2% solution of copper sulphate. NAPPER states that this epiphytic habit of the *F. lignosus* rhizomorphs renders it possible, by this periodical treatment, to bring a stand of young rubber through a heavy attack of *F. lignosus* without losing more than 20% of the trees that have been attacked. The rhizomorphs of the other two members of the Malayan root disease complex, *G. pseudoferreum* and *F. noxius,* are epiphytic only for some 18 inches in advance of penetration, so that a proportionately greater loss of trees infected by these two fungi is inevitable. Owing to the fact that these fungi generally occur sparsely by comparison with *F. lignosus* on jungle sites, however, the efficiency of the control method is not seriously impaired. In this way, root disease can be eliminated before the roots of the trees have expanded into their full planting sites (after some 10 years); once the roots of adjacent trees begin to interlace, spread of infection becomes at once more rapid and more dangerous.

A noteworthy feature of this method is the rejection of trenching, with the realisation that, as spread of these diseases takes place mainly through root contact, trenching will be unnecessary before the root systems of the young trees have expanded fully into their planting sites and made contact with those of their neighbours; by this time, the majority of the buried sources of infection should have been disclosed and removed at the periodical tree-to-tree inspections. Trenching has not, therefore, been advocated by NAPPER (1937), except for control of disease in mature plantations (*see* next chapter).

**Infection of Moribund Stump Roots after Felling:** — These discoveries of NAPPER'S, whilst throwing doubt upon the hypothesis of air-borne spore infection of jungle stumps, provided no explanation to account for the undoubted association between outbreaks of root disease in plantation crops and the operations of thinning-out or felling of shade trees. Gradually, however, a suspicion grew up that an alternative mode of infection was possible, and even probable, *viz.* a direct infection from the soil of the moribund but still living roots of the stump, the resistance of which to infection had been sharply lowered by the act of felling. This implied, of course, the existence of inoculum dormant before the actual felling, either in the form of infected timber lying adjacent to the roots, or as root lesions that had been immobilised by

the host defence mechanism. In the disturbance of the soil incidental to felling and clearing of the virgin jungle, mycelium lying dormant in buried timber might well be roused into activity, especially in low-lying coastal areas where clearing and draining operations resulted in the lowering of a water table too close to the surface for successful planting. The occurrence of latent infections, or localised lesions, of *Fomes lignosus* in the roots of apparently healthy rubber trees was demonstrated by DE JONG (1933) in Sumatra, who states, in the English summary of his paper: "it was observed that *Rigidoporus** decay frequently stops without treatment and of its own accord. In such cases the decayed patches become surrounded by callus and eventually heal over completely. It is striking that the process of recovery ordinarily started at about the time when the wood used for inoculation had itself disappeared through decay. In certain instances, however, it was observed that *Rigidoporus* decay continued to develop after the exhaustion of the original inoculating material. This situation probably results when the decay has progressed to such an extent, before the disappearance of the wood used for inoculation, that the tree becomes seriously weakened."

SHARPLES (1936) obviously appreciated the occurrence and significance of the fall in root resistance to infection after felling, for he remarks: "Another point to remember is that a vigorous rubber tree displays a certain amount of resistance to attacks of *G. pseudoferreum* by the production of adventitious roots, but there is no resistance offered by the part of a rubber tree left in the soil after the upper parts have been removed by thinning-out. When the trunk of a tree is removed, the roots do not necessarily die with great rapidity. However, they become moribund and ultimately death follows. The loss of resistance to the attacks of the fungus may be considered an additional factor which will lead to the rapid spread of root disease after thinning-out." The same point was also taken into account by NAPPER (1937) in a discussion of replanting policy; concerning areas of old rubber that are apparently healthy at the time of felling he remarks: "Of greater interest are the losses which occur in *untreated* soil, *i.e.* in areas of the clearing which were apparently healthy at the time of felling. These losses are invariably caused by contact with infected roots belonging to the original stand, but the existence of such roots in 'healthy' areas is sometimes rather difficult to explain. In general, however, they may be regarded as old infections in which the disease has lain dormant for very many years until brought into activity again by the process of felling. The causes of dormancy are still somewhat obscure. The most common cause in the field appears to be continuous saturation with water. This is shown by the fact that losses of the type under consideration are most abundant in low-lying coastal areas where the

* *Rigidoporus microporus* is a synonym of *Fomes lignosus*.

water table was originally high, but has been extensively lowered in the process of replanting. The causes of dormancy on inland soils are less important and not so clearly understood." A similar conclusion has been voiced by MURRAY (1938) for rubber areas in Ceylon: "When a stand of old Rubber, in which no case of root disease has ever been recorded, is felled, it was at first supposed that the root fungi were absent, and that there would be no risk of the young plants becoming infected from old roots left in the ground. Recent experience has shown that this is not a safe assumption .... in every investigated case .... it has been possible to trace the source of infection to an old Rubber root bearing the typical rhizomorphs, the fungi concerned being usually *Fomes lignosus* or *Poria hypobrunnea.* This proves that the fungus must have been present before the old trees were felled, and it was probably present in the wood of a root in a condition of what may be termed 'subdued parasitism'. . . . When the trees are felled the equilibrium is upset."

Proof of this contention, however, was published neither from Malaya, Sumatra nor Ceylon, but came from East Africa, in two contributions by LEACH (1937, 1939), the importance of which it is difficult to exaggerate. In the first paper, LEACH recorded his observation that whereas the percentage of trees killed by *Armillaria mellea* in virgin forest was very small, even in a pure stand of a susceptible species, yet when the forest was cut down, the roots of many species became extensively invaded by *A. mellea;* this implied a breaking-down of root resistance to infection. A similar observation had previously been published by WALLACE (1935*b*) from Tanganyika Territory. In his second paper, LEACH (1939) reported various experiments designed to test the correctness of this conclusion. Twenty-six species of native tree were selected for experiment; in order to simulate the act of felling, lateral roots ½-1½ inches in diameter were sawn through at a distance of 4 feet from the trunk, at the time of inoculation. Two individual trees of each species were tested for resistance to attack by placing pieces of infected *Glyricidia sepium* root in contact with the roots of the tree. Six roots of each tree were inoculated, three being cut through above the point of inoculation, and three being left uncut; the roots were examined 4 months later. Examination of the *uncut roots* showed that roots of 6 species were never invaded by *A. mellea* and appeared to be completely resistant to attack. The roots of all other species were invaded, but, with only two exceptions, were able to confine the parasite within narrow limits, apparently by the formation of gum barriers and callus. Examination of the *cut roots* showed that roots of 24 out of the 26 species were susceptible to invasion; in all 24 of these species, the fungus travelled freely down the roots, though in 5 species *some* of the roots still showed resistance. LEACH compared the resistance shown by the uncut roots in this experiment with that

demonstrated in the Myrobolan plum by THOMAS (1934), in his study of infection of susceptible and resistant hosts by *A. mellea.*

As a result of these experiments, LEACH (1939) concluded: "This experiment . . . . indicates that trees growing near dead stumps in forests may have many localised lesions of *Armillaria* dormant in their roots and that the fungus in these lesions may become active when the forest is felled for a plantation crop. The fungus may spread from these localised lesions even though the roots of the original dead stumps may have been rotted by *Armillaria* beyond the stage in which they would be capable of causing infection." LEACH records two other observations of particular interest: "Some roots on the 'Msopa' tree.... had been invaded at two points close together but on opposite sides. Such roots had lost the power of resistance below the points of infection, *Armillaria* having travelled freely down the root but not up to the crown. . . . In Nyasaland, *Eucalyptus* trees are not considered susceptible to *Armillaria*. . . . Observations showed that a *Eucalyptus* tree forms localised lesions when invaded by *Armillaria* similar to those described for the 'Msopa' tree. If the *Eucalyptus* tree, however, is situated on ground containing a mass of diseased 'Muula' roots it sometimes succumbs to *Armillaria* root disease, its resistance being undoubtedly lowered by the large number of invasions made throughout its root system."

**Ring-Barking and Tree Poisoning Methods for Reducing Root Disease Losses after Clearing:** — In addition to the important observations just described, LEACH (1937) announced another discovery, which suggested a simple and very practical method for avoiding such losses. In a microscopical study of the pathological histology of infected tea seedling roots, LEACH noticed that hyphae of *A. mellea* were virtually absent from the root cortex, but plentiful in the pith; whereas the cortex was devoid of starch, the pith was well supplied. He concluded, therefore, that *A. mellea* required roots with a high carbohydrate content for its development. In a search for *A. mellea* on the roots of felled stumps of "Muula" (*Parinarium mobola*) trees, which are especially liable to infection by *A. mellea* after felling, LEACH selected for examination 12 trees that had been ringed some time before felling (and in which the roots must have been depleted of carbohydrate before the trees were felled), and 24 non-ringed trees as controls. Twenty out of the 24 stumps or trees not ringed before felling were found to have roots (varying from 6 to 13 per stump) infected by *A. mellea;* the other 4 had roots infected by "dry-rot" fungi of the *Rhizoctonia bataticola* type. Of the 12 stumps of trees ringed before felling, one stump showed one root that might have been infected by *A. mellea,* whereas all other roots showed a "dry-rot" due to saprophytic fungi. LEACH therefore suggested that if the

forest trees were ringed well in advance of felling, their roots would rapidly become devoid of starch, would die early and be invaded by harmless saprophytic fungi instead of by *A. mellea.* In the second paper (1939), he reported experiments demonstrating that once roots or woody prunings had been invaded by saprophytic fungi, they could not be entered by *A. mellea.*

In conclusion, LEACH (1939) suggests an explanation for the association of *A. mellea* with the stumps of particular native trees in Nyasaland: "The results obtained in the experiment on the susceptibility of indigenous trees, showing that nearly all species in a mixed forest are susceptible to *Armillaria* after the roots are severed, raises the critical question why a few only of these species are usually associated with this fungus as a source of infection in tea estates. I suggest that many trees escape infection because their roots die rapidly after felling before *Armillaria* reaches them. Once dead, and invaded by saprophytes, these quick-dying roots cannot be invaded by *Armillaria.* Unless, therefore, roots of one of the quick-dying species are in close contact with a centre of infection at the time of clearing a mixed forest, they are unlikely to become infected before they die. . . . The species of tree considered the most dangerous as sources of infection by *Armillaria* are those of which the roots die very slowly after felling. In January 1938 a root of 'Muanga' (*Afroformosia*) was found alive at a depth of 3 ft. in a block of tea planted in 1934. 'Muula' (*Parinarium mobola*) is another such tree. . . . The ability of the roots of 'Muula' to keep alive so long after felling probably explains why a pure stand forest of 'Muula' trees often gives rise later to such widespread damage in tea gardens, because starting from a few scattered infected stumps, as in the mixed forest, *Armillaria* can spread unimpeded along a network of *moribund,* but still susceptible, roots." TUNSTALL (1940), commenting upon the association between stumps of felled shade trees and outbreaks of root disease of tea due to *Fomes noxius* and *Ustulina zonata* in North East India, remarked that the stumps of hardwood trees, such as Nahor (*Mesua ferrea*), Sal (*Shorea robusta*), and Khair (*Acacia catechu*), were more frequently associated with outbreaks of root disease in the surrounding tea than were those of soft-wooded trees, which decayed more rapidly.

The interest aroused by LEACH's discoveries has been quickened by NAPPER's (1939) announcement that stump poisoning of rubber by sodium arsenite produced a result apparently analogous to that of ring-barking, by killing the roots of the stumps and so rendering them liable to invasion by saprophytic fungi rather than by *Fomes lignosus.* This result was obtained in the course of an experiment designed to test out methods for prevention of root disease on a replanted area (*see* next chapter). At the same time, NAPPER described another experiment designed to compare LEACH's ring-barking method, arsenite poisoning

by injection, (i) of the living trees before felling, (ii) of the stumps after felling, and an untreated control. Although results from this particular experiment in terms of incidence of root disease after replanting are not available, NAPPER's observations on starch content of the roots in the different series are pertinent to the present discussion. The ring-barking and tree poisoning were carried out early in June, from 4 to 6 months before felling, and the stump poisoning shortly after felling. Comparative estimates of the starch content were made at the end of September, and again early in December; root sections were cut longitudinally, and the exposed surfaces planed, stained with iodine-potassium iodide solution, and compared with similarly treated sections from standing trees. It was found by visual grading that approximate losses of starch were as follows: —

(i) In trees ring-barked 4½ months before felling, the roots had lost 52% of their starch content at 3½-4 months, and 86% at 6 months after treatment.

(ii) In trees frill-girdled and poisoned with sodium arsenite 4 months before felling, the roots had lost 98% of their starch at 5½ months after treatment.

(iii) In stumps poisoned by injection with sodium arsenite immediately after felling, the loss was 65% at 2 months after treatment.

(iv) In untreated stumps the loss was only 4% during the first 2½ months after felling.

NAPPER observed a fairly close relationship between the rate of loss of starch from the roots and the rate of invasion by saprophytic fungi.

**Air-borne Spore Infection of Exposed Wood Surfaces:** — So much, therefore, for the evidence for direct infection of the roots of felled stumps via the soil. Such evidence, although impressive, by no means excludes the possibility that infection of the roots may develop from spore invasion of the exposed cut surfaces of the stumps; the extent and frequency of such hypothetical spore infection can only be gauged by direct experiment. There is some evidence for the occurrence of such air-borne infection by *Ustulina zonata,* which is well known not only as a root parasite of tea and rubber in Malaya and Ceylon, but also as a wound parasite of the stem, gaining entrance through spore infection of pruning snags, and of hoe cuts in the stem just above ground level. *Fomes noxius* can also, apparently, behave in a similar way; NAPPER (1938*a*) has described an apparent instance of spore infection of felled rubber logs used for terracing, *viz.*: "At about six months after felling numerous cases of Brown Root Disease appeared among bush cover plants (*Tephrosia vogelii*) established below the logs on the banks of the terraces. These infections were thought at first to be caused by contact with infected roots overlooked during the clear-

ing of the original stand. Field investigation showed, however, that this was not the case; in every instance the source of infection was found in a neighbouring log. There was no evidence to suggest that these logs had themselves been infected by contact with the soil or with buried infected roots. It was therefore concluded that infection had been caused by wind-blown spores." The question has been recently revived by GADD (1940), in connection with the aftermath of felling shade trees on tea estates in Ceylon, concerning "an estate which felled about 6,000 *Grevillea* trees which had been grown as shade for tea. About two years after felling 30% of the stumps had given rise to Brown Root Disease with the result that 3,000 bushes had to be removed. The source of infection was attributed to wind-carried spores which presumably found lodgment on the cut surfaces of the stumps."

The discussion of this controversial question of stump infection after felling may be concluded with NAPPER'S (1940) account of yet another factor affecting the incidence of root disease in young plantations on cleared jungle sites: "The most striking fact revealed was the reduced incidence of root disease during the early years after planting in areas *cleared without burning,* as compared with areas burnt off in the usual way. . . . Up to the end of the third year from planting (which is as far as the present records go) it appears normal to expect at least twice as many root infections in burnt as in unburnt areas, and in one experiment a ratio as high as 5 to 1 was observed. No satisfactory explanation of the phenomenon has yet been advanced. It was thought at first to indicate a delayed attack in the unburnt areas, due to the greater bulk of timber left after clearing in these areas as compared with areas burnt off in the normal way. Recent observations suggest, however, that this is not the case, but that burning actually *encourages* the spread of root infection among the root systems of the jungle trees during the susceptible period after felling."

**Economics of Root Disease Control:** — In the formulation of a policy for root disease control on any area, it is not the mycologist but the economist who has the last word. A valuable feature of the experiments on root disease control carried out by the Rubber Research Institute of Malaya has been the recording of costings for all operations. In Sumatra DE JONG (1933), as a result of extensive observations and experiments on estates where *Fomes lignosus* was the only important root parasite of rubber, concluded that natural recovery of young rubber from infection by *F. lignosus* was commoner than generally supposed, and that conclusions based on a single root examination might exaggerate the importance of this root disease. Much of the superficial or epiphytic mycelium found on the roots at any examination might never achieve infection; even established lesions might become surrounded by callus and heal over completely. DE JONG therefore

criticised NAPPER's (1932*a*) earlier conclusions on the score that an estimate of the root disease situaton in any area should not be based upon incidence of mycelium on the roots, nor upon a single examination for the presence of root decay, but rather upon repeated examinations to show the progress of decay, or, better still, upon records of mortality due to the disease. He therefore refused to make any general recommendations for control of *F. lignosus,* preferring to consider individual outbreaks of root disease in relation to local conditions on the area concerned.

NAPPER has justified his policy of periodical tree-to-tree inspection by pointing out that the same treatment will bring not only *F. lignosus* and *F. noxius,* but also *Ganoderma pseudoferreum* (with which DE JONG in Sumatra was not concerned) under control; *G. pseudoferreum* is likely to cause most serious losses in plantations of 10 years old and upwards if preventive measures are not taken earlier, as by this time the root systems of adjacent trees are all in contact. This view has been upheld by SHARPLES (1936): "If DE JONG's investigations can be confirmed by observations in Malaya, it is obvious that on lightly infected areas the disease caused by *F. lignosus* will not call for special treatment, and that it may be possible, as certain planters claim, to limit treatment to removing the roots and stems of the trees killed by the fungus and re-supplying immediately. But if this type of treatment is undertaken and no attention is given to eradicating disease knots of *Ganoderma pseudoferreum* in the early years, then it can only be expected that more time must be spent and further expense incurred when the trees are about the age of ten years. It cannot be emphasised too often that the recommendations now being made for treatment of *F. lignosus* are largely dependent on the fact that such treatment will also result in the early extermination of disease knots of *G. pseudoferreum.*"

*Chapter 13*

# CONTROL OF ROOT DISEASE IN PLANTATION CROPS: IN MATURE PLANTATIONS AND ON REPLANTED AREAS

The amount of disease in the mature plantation will depend upon the previous vegetation, the method of clearing, and the thoroughness with which measures for eradication of root disease have been carried out in the earlier years of the plantation. Once the roots of the plantation trees have expanded fully into their planting sites and made contact with those of their neighbours, the spread of root disease becomes more rapid and more dangerous. It has then to be decided whether to undertake *ad hoc* control measures to prevent further spread of root disease, and if possible to eradicate it, or to clear and replant. Replanting may be deemed advisable not only on the score of root disease, but also because yield has fallen off for other reasons, or compares unfavourably with that of more recent plantations. Thus SHARPLES (1936) remarks: "We may justly inquire why, during depressed financial periods, a policy of replanting uneconomic areas should be undertaken. The reply is found in the probable yields of rubber to be obtained by utilising modern methods of planting-up bud-grafted material, *i.e.* trees which have been proved definitely superior and found to possess all the desirable properties. These strains of rubber trees are expected to give greatly increased yields, even to the extent of twice or three times the amount given by the ordinary mixed material planted in past years."

**Root Disease Control in Mature Plantations:** — Let us suppose that a decision has been taken to keep on the standing plantation for a further period. Even if replanting has been postponed indefinitely, root disease control measures should be designed not merely to limit the spread of disease, but to eradicate it wherever possible; in this way, the cost of eventual clearing and replanting will be reduced. The isolation of diseased areas by means of a trench should therefore be supplemented by removal of dead trees and all buried infected material from the area enclosed by the trench, as originally recommended by PETCH (1921). PETCH directed that the isolation trench should enclose not only the diseased tree, but also a complete ring of surrounding trees, even although the latter were apparently healthy. The trench had to be dug to a depth of about 2 feet and had to sever all lateral roots; in deeper soils, a greater depth of trench might be necessary. Further directions were given as follows: "It is now becoming customary to open up and examine the roots of trees which are included within the isolation trench, in order to determine whether they have already been attacked. It is of course impossible to follow

up the roots to their extremities, but enough can be done to show whether the tree is seriously affected. The roots should be exposed for a radius of about three feet from the stem, and the tap root to a depth of about two feet. . . . If upon examination the tap root is found to be decayed, the tree should be removed. If the fungus is found advancing towards the collar on one or two laterals, these may be cut back into sound tissue, and the diseased laterals dug out. It must be borne in mind that the mycelium usually travels along the underside of the laterals, especially when the upper side is exposed; this is particularly so in the case of *Fomes lignosus.* In the latter disease, the external strands of mycelium fairly frequently extend over the surface of the root in advance of the penetration of the fungus. The part covered by the youngest mycelium may consequently not have been attacked, or only attacked to a slight depth. In such cases, the mycelium and any underlying decayed bark may be cut away and the wound treated. This method is especially useful when the tap root only has just been attacked. In Ceylon it is usual to dress the roots from which mycelium has been scraped off with Brunolinum, or tar, while in the Straits Settlements, Bordeaux paste has been used. It must be remembered that the mycelium travels inside the root as well as on its surface, and consequently, if the decayed parts of the root are not cut away, any treatment is useless. The method is said to have been attended with great success, trees which bore the mycelium of *Fomes lignosus* having been completely cured." It is interesting to see in this early procedure, which PETCH declared to be applicable also to control of the rubber root diseases caused by *F. noxius* and *Ustulina zonata* in Ceylon, the germs of the method later to be developed so successfully by NAPPER in Malaya for a different purpose, *i.e.* control of root disease and eradication of the causal fungi in *young* plantations.

PETCH's directions for trench isolation and treatment of a diseased area evidently proved fairly satisfactory in practice, for little has been added to them; they were repeated by SHARPLES and SANDERSON (1931) in their recommendations for control of *Ganoderma pseudoferreum* on old rubber areas in Malaya. For correct siting of the isolation trench, SHARPLES (1936) has given the following instructions: "The main requirement of an isolation trench is that it shall be cut outside the advancing limits of the patch. If, therefore, in cutting the trench all the roots severed are healthy, the trench must be fulfilling this requirement. If, however, diseased roots are encountered, the trench is known to be incorrectly placed. . . . The diseased roots are the indicators for the location of the trenches, and these must be taken further and further away from the diseased patch until all roots severed are healthy."

An improvement in trench maintenance was suggested by NAPPER

(1937), who pointed out that the classical method of keeping the trenches permanently open by clearing out all silt and vegetable debris at regular intervals was completely effective only where a shallow soil overlay a subsoil impervious to roots. In soils of normal depth, new rootlets produced from the ends of the severed laterals found their way down the sides and under the floors of the trenches, and within a year or two of the original digging root contact was again established between diseased and healthy areas. The trenches thus had to be dug progressively deeper, and the work became more difficult and more expensive at each digging. NAPPER therefore suggested that *trenches should be refilled as soon as they had been dug.* All new root contacts would then be established *above* the floors of the trenches, and efficiency could be restored at intervals by redigging the trenches to their original depth. Such refilled trenches were usually invaded by small roots within six months of cutting and refilling, but the spread of disease through this maze of rootlets was slow, and it was unnecessary to dig out the trenches more often than once every 1½-2 years. At each redigging, the root sections had to be examined in the usual way, and any infected roots passing beyond the trench had to be followed up and removed.

For controlling the root disease caused by *Poria hypolateritia* in old tea areas in Ceylon, GADD (1929*a*) recommended trenching, with removal and destruction of all bushes within the isolation area — since these would sooner or later be killed by the disease if left standing. In a later paper, GADD (1936*a*) observed that whereas *Fomes noxius* could usually be eradicated by the simple expedient of uprooting the diseased tea bush and removing the source of infection, this procedure was quite inadequate to check the spread of *Poria hypolateritia.* This was attributed to the fact that whereas *F. noxius* was a quick-killing fungus, and usually killed an infected bush before the roots of neighbouring bushes had become infected, *P. hypolateritia* was a slow-killing fungus, and had usually become well established on the roots of surrounding bushes before the first infected bush was visibly affected by the disease. Later, GADD (1937) discussed the failure of current control methods to check the spread of *P. hypolateritia* in old tea, which he attributed to the placing of too much reliance upon isolation trenches, at best a passive defence. He declared that control of this fungus could be achieved only by removing a ring of healthy bushes around every diseased one.

GADD'S (1936*a*) conclusion is supported by TUNSTALL'S (1940) estimate of the root disease situation in the tea plantations of North East India, where the two most important root diseases appear to be those caused by the quick-killing but slow-spreading fungi, *Fomes noxius* and *Ustulina zonata.* TUNSTALL no longer recommends the digging of isolation trenches, deeming it sufficient to remove the diseased tea

bush, together with all dead wood from the soil immediately surrounding it. Healthy bushes need be removed, according to TUNSTALL, only when their roots occur in very close proximity to the roots of a diseased bush.

**Root Disease Control on Replanted Areas:** — Any decision concerning the extent of measures for root disease eradication to be taken prior to replanting must be dictated by economic considerations. The cost of the work varies from country to country, from district to district, and even from one estate to another, according to soil, situation, and labour available, etc.; more important and more variable, however, is the expectation of root disease in the replanted stand. Few experimental results are available for guidance in making such decisions, so that an experiment carried out by NAPPER (1938*a*, 1939-40) on rubber in Malaya, and another by CRONSHEY and BARCLAY (1939) on rubber in Sumatra will be fully described.

The site of NAPPER's replanting experiment was a rectangular block of 80 acres in old rubber, where disease patches occupied at least 50% of the total area. The main parasite was *Ganoderma pseudoferreum*, but *Fomes lignosus* and *F. noxius* were also present. Six treatments with 5 replications were arranged in randomised block design, giving a plot unit of 2⅔ acres; the treatments were as follows: —

*A*. Uniform digging to 18 inches, all roots being removed to this depth whether healthy or diseased.

*B*. As *A*, but digging only to 10 inches.

*C*. Disease patches dug over to a depth sufficient to ensure complete removal of infected roots. Remainder of the area dug uniformly to 10 inches without collecting roots.

*D*. Disease patches dealt with as in *C*, but remainder of the area left undug. Apparently healthy trees were felled by jack or grubber to ensure removal of the boles and larger laterals, and to give a further opportunity for root examination.

*E*. No systematic digging. Diseased trees were dug out individually, all infected roots being followed up and removed. Healthy trees were dealt with as in *D*.

*F*. No digging or removal of stumps. Trees (both healthy and diseased) were cut off at ground level, the stumps being then poisoned by injection with sodium arsenite.

The different treatments were completed by the end of 1937, and the whole area was then planted with rubber; after planting, the usual periodical tree-to-tree inspection for discovery and eradication of sources of root disease infection, as developed for young plantations on virgin land (*see* above, p. 111), was carried out over the whole experimental area. The total incidence of root disease infection in

the young rubber up to the end of the first and second years after planting, respectively, is given below in Table 16. NAPPER also gives numbers of bush cover plants killed by disease under the different treatments, but as these figures run in much the same order as those for infection of the rubber, they need not be quoted here.

TABLE 16. *Incidence of root disease in young rubber on replanted area in 1938 and 1939:* —

| | NUMBER OF RUBBER TREES INFECTED BY: — | | | | | |
|---|---|---|---|---|---|---|
| TREATMENT PRIOR TO REPLANTING | FOMES LIGNOSUS | | GANODERMA PSEUDOFERREUM | | FOMES NOXIUS | |
| | 1938 | 1939 | 1938 | 1939 | 1938 | 1939 |
| A | 8 | 31 | 1 | 15 | 1 | 4 |
| B | 13 | 55 | 5 | 21 | 1 | 3 |
| C | 17 | 72 | 1 | 9 | 1 | 7 |
| D | 31 | 102 | 0 | 6 | 1 | 3 |
| E | 23 | 96 | 0 | 12 | 2 | 6 |
| F | 12 | 49 | 2 | 22 | 2 | 5 |

Comment upon the results obtained by the end of the first year after planting (1938) is best given in NAPPER'S (1939) own words: "In the first place they provide a striking demonstration of the fact, which has gradually become apparent in recent years, that root disease control in connection with replanting is not a single problem, but a combination of two separate and unrelated problems which require separate consideration when planning a policy of control, *viz.*: —

(*a*) Control of root disease in areas affected by root parasites in the original stand, and

(*b*) Control in areas outside the old root disease patches, *i.e.* in areas carrying healthy trees at the time of felling.

"The site chosen for the experiment was well adapted to effect a separation and to permit separate study of these two problems, since the parasite mainly responsible for damage in the original stand was *Ganoderma pseudoferreum,* whereas the parasite causing trouble where healthy roots are left to rot in the soil is invariably *Fomes lignosus* (*see* Annual Report for 1936, p. 83). It was expected, therefore, that the rates of incidence of *Ganoderma pseudoferreum* under the various treatments would provide a measure of the relative efficiencies of the treatments in dealing with problem (*a*) and would vary inversely with the amounts of digging carried out *within* the boundaries of the root-disease patches, whereas the rates of incidence of *Fomes lignosus* would provide a similar but independent measure of the efficiencies of the treatments in dealing with problem (*b*) and would vary inversely with the amounts of digging carried out *outside* the boundaries of the root-disease patches. Reference to columns 7

and 8 of Table 1* will show how closely this expectation has been realised. The only inconsistency is the low incidence of *Fomes lignosus* in treatment *F*, and here an additional factor had been introduced, *viz.* the poisoning of the stumps of the trees after felling by injection with sodium arsenite.

"The effect of stump-poisoning in lowering the incidence of *Fomes lignosus* in the *F* plots is a matter of considerable practical interest. The method has often been suggested by non-technical observers as a means of controlling root disease at the time of replanting, but has usually been regarded by its advocates as a method of destroying roots already infected by root parasites, *i.e.* as a method of dealing with problem (*a*). It is, of course, useless for this purpose, a fact which is confirmed in the present experiment by the high incidence of *Ganoderma pseudoferreum* in treatment *F*. The present results show, however, that as a method of dealing with problem (*b*) the method merits serious consideration. More green timber was left to rot in the soil in treatment *F* than in any other treatment included in the experiment, yet the incidence of *Fomes lignosus* under this treatment was only half the incidence under treatments *D* and *E* in which the chances of infection and spread were greatly reduced by the removal of the stumps and laterals of the healthy trees, and no higher than in treatments *B* and *C* in which all healthy roots were extracted to a depth of 9 inches. . . . .

"The success of the method depends on the fact that poisoning hastens the onset of decay, and therefore shortens the period between felling and invasion by saprophytic organisms during which the roots are green and abnormally susceptible to attack by *Fomes lignosus*. It is during this period that the sources of infection are developed which later give rise to losses in the replanted stand. Shortening the period of susceptibility reduces both the number and size of these sources, and thus provides a useful measure of control. It is still difficult to explain satisfactorily where the *Fomes lignosus* comes from. Some undoubtedly originates from dormant sources which existed in the original stand. Spore infection of the partially exposed and highly susceptible green root-fragments cannot, however, be entirely disregarded."

NAPPER'S conclusions on this experiment may be summarised by saying that trouble with *Ganoderma pseudoferreum* in the young plantations occurred only on the sites of root disease patches in the old stand, and could be dealt with by the extraction of all buried infected roots on such sites; trouble with *Fomes lignosus*, on the other hand, was the result of leaving roots of healthy trees in the soil after felling, and constituted, therefore, the same problem as that encountered in young plantations established on jungle sites. Concern-

*Figures reproduced in Table 16, above.

ing the infections by *Fomes noxius*, NAPPER stated that nearly 60% of these were directly traceable to contact with diseased rubber logs lying on the surface of the soil; these logs had undoubtedly become infected after felling, most probably by wind-blown spores of the fungus (*see* above, p. 117).

At the end of the second year (1939) of this experiment, the figures for total root infections ran in the same order as those obtained at the end of the first year, and so require no further comment. NAPPER (1940) was unable to decide whether treatment *F*, stump injection with sodium arsenite, would eventually prove more economical than the methods for dealing with the root systems of healthy trees adopted in treatments *B*, *C*, *D* and *E*. He pointed out that where infection by *F. lignosus* did occur under treatment *F*, it was more expensive to deal with, and the higher cost per point treated might outweigh the benefit derived from reduction in number of infections. A full discussion of the costings for this experiment up to the end of the second year after planting has been included in this report by NAPPER (1940).

CRONSHEY and BARCLAY'S (1939) replanting experiment, of factorial design, was carried out on the site of a 25-year old rubber plantation on a flat coastal area of clay soil in Sumatra. The old stand had originally been planted at the rate of 121 trees to the acre, had been thinned to 80, and at the time of clearing averaged less than 60 trees to the acre. Collar inspection at clearing showed 15% of the remaining trees to be diseased, *Fomes lignosus* being the predominant parasite. Details of the experimental treatments (*see* Table 17) are given by CRONSHEY and BARCLAY, as follows. Stumps were removed with stump pullers, so that root collars and parts of the tap root and larger laterals were extracted. Roots were removed by "changkolling" (a changkoll is a native hoe) to a depth of 15-18 inches. In "holing", planting holes 2× 2 × 2 feet were dug, and refilled with top soil free of roots. Losses (at the tend of 2 years after planting) amongst the young rubber from root disease, declared by CRONSHEY and BARCLAY to be due almost entirely to *Fomes lignosus*, are given in Table 17.

These results provide a clear-cut answer to most of the questions that this experiment was designed to elucidate. The presence of cover reduced mortality by about 60% on an average of all comparisons. This confirms the earlier conclusions of NAPPER (1932*a*). As might have been expected, "holing" has reduced the incidence of disease. On an average of all comparisons, the removal of stumps and roots has reduced mortality to little more than half that occurring when neither stumps nor roots were removed. An interesting difference is revealed by the comparison of losses following the two treatments "stumps left, roots removed" and "stumps removed, roots left",

TABLE 17. *Mortality in two-year-old rubber due to root disease (caused almost entirely by Fomes lignosus)*: —

| | STUMPS LEFT ROOTS LEFT | STUMPS LEFT ROOTS REMOVED | STUMPS REMOVED ROOTS LEFT | STUMPS REMOVED ROOTS REMOVED | TOTALS |
|---|---|---|---|---|---|
| *Clean weeded — no holing.* | 729 | 611 | 917 | 524 | 2781 |
| *Clean weeded — holing.....* | 671 | 518 | 712 | 400 | 2301 |
| *Cover — no holing.........* | 406 | 421 | 321 | 194 | 1342 |
| *Cover — holing ...........* | 293 | 298 | 168 | 111 | 870 |
| *Totals ...................* | 2099 | 1848 | 2118 | 1229 | 7294 |

according to whether the area is clean weeded or under cover. CRONSHEY and BARCLAY have not commented upon this curious discrepancy, for which the following explanation is here suggested. In the clean-weeded areas, removal of roots, leaving stumps, has decreased disease losses as might have been expected, on the assumption that roots form the more widely dispersed source of inoculum. But removal of stumps, leaving roots, has actually increased disease mortality above that where stumps and roots were left. Is it not possible that violent removal of the stumps has increased the susceptibility of the roots left in the soil to infection by latent inoculum of *F. lignosus*, by analogy with the increased incidence of disease on virgin jungle areas burnt after clearing, as compared with unburnt areas (NAPPER, 1940)? In areas under cover, on the other hand, removal of roots but not stumps has not significantly affected the incidence of infection, whereas removal of stumps but not roots has substantially reduced it. To explain this paradox, let us assume that the roots provide more sources of infection, but that these are of smaller volume, whereas the stumps provide fewer but more massive sources of infection. Under clean weeded conditions, where no obstacles are interposed between the roots of the rubber and the inoculum, the roots might be expected to produce the greater number of infections; under cover, however, the "baffling" effect of the cover roots upon the spread of the rhizomorphs, as postulated by NAPPER (1932-34), might prevent the fungus reaching the rubber from many of the smaller sources of infection provided by the roots, so that the fewer but more massive sources of infection provided by the stumps might ultimately produce the greater number of infections.

CRONSHEY and BARCLAY themselves comment as follows upon their results: "As is shown by the column totals in Table III*, stump-pulling and changkolling are closely interrelated, neither being of much

* Reproduced above as Table 17.

value in the absence of the other. Collectively, however, they have reduced the losses by nearly a half, and it is noticeable that the effect has been larger when other favourable treatments, holing and the establishment of a cover, were also done. In general, the combined effect of the favourable treatments is greater than the sum of their single effects, the percentage reduction being considered as the correct measure of efficiency." They also pointed out that the presence of cover had resulted in a slight reduction in growth of the young rubber, as estimated by increment in diameter of the stem, and suggested that the clean weeding of circles around the trees or of strips along the rows might prove a satisfactory compromise.

On replanted rubber areas in Ceylon, according to MURRAY (1938), the mortality in young rubber from root disease (due almost entirely to *F. lignosus;* occasional outbreaks due to *F. noxius* and *Poria hypobrunnea*) is evidently much lower than that in Malaya or Sumatra. Prior to the replanting of areas occupied by disease patches due to *F. lignosus* in the old stand, MURRAY recommended the entire removal, if possible, of all old roots; on healthy areas, however, laterals might be left to decay *in situ.* Infection amongst the young rubber trees due to the development of latent inoculum of *F. lignosus* adjacent to or in the laterals of felled stumps in such previously healthy areas could be eliminated, according to MURRAY, by prompt treatment of visibly-affected young trees and removal of the source of infection. MURRAY justified the adoption of this procedure as follows: "This policy could only commend itself if the numbers of plants so lost were small, and if the knots of infection were disclosed before the fungus could spread a great distance. In most of the replanted clearings of which I have knowledge the number of casualties due to root disease amounts so far to considerably less than 1% of the total stand. Some of these clearings are quite recent, but others are up to 8 years of age. Even 1% is an insignificant proportion especially as the initial stand is usually much greater than the final stand aimed at. In the first two years or so the casualties can, of course, be replaced with supplies." MURRAY goes on to suggest that the root disease fungi are likely to spread actively along the laterals of the old stand left in the ground only for the first few months after felling, whilst the roots are still fairly fresh; as for spread along the roots of the young rubber, this should not become dangerously rapid until the root network of the rubber has been fully developed, at an estimated age of 12-15 years. If the existence of sources of infection has not been revealed by this time, such sources may be regarded as dormant, and therefore comparatively harmless.

In a further communication, MURRAY (1939) reported data derived from replies by 156 estates to a questionnaire on replanting policy. Lateral roots had been removed from the ground prior to re-

planting on 2465 out of 8124 acres; loss due to root disease fungi (chiefly *F. lignosus* but a little *F. noxius* and *Poria hypobrunnea*) was approximately 0.06% where laterals had been removed, and 0.14% where they had been left in the soil. In the following year, MURRAY (1940) declared the mortality from root disease to reach a maximum in the second or third year from planting, and thereafter to show a marked decline; although this was largely due, no doubt, to the disclosure and eradication of sources of infection by the method just described, there was evidence that fungal activity tended to die down even where infected old roots were left in the ground. No doubt, too, the resistance of the rubber plant to *F. lignosus* increased with age (DE JONG, 1933). MURRAY also stated that several estates with a high incidence of *F. lignosus* in young replantings had been advised to undertake the routine collar inspection treatment developed by NAPPER in Malaya, and that this had proved quite feasible under conditions in Ceylon; it was doubtful, however, whether adoption of this treatment would prove to be economically sound. MURRAY'S policy for replanted areas in Ceylon therefore seems to have been justified by the low mortality due to *F. lignosus* amongst the young rubber in that country, and by the absence of *Ganoderma pseudoferreum;* a similar conclusion had been reached earlier by DE JONG (1933) in Sumatra, and SHARPLES (1936) has pointed out that a similar policy might be followed in Malaya were it not for the widespread occurrence of the more dangerous root parasite, *Ganoderma pseudoferreum.*

A suggestion that susceptible bush covers might be employed as "indicators" of root disease in areas of young replanted rubber was made by BERTRAND and MINOR (1937) in Ceylon. They recommended a mixture of three bush covers, so as to reduce incidence of stem and branch diseases, which would spread more rapidly in a pure stand of a single species. MURRAY (1938) criticised this proposal on the score that it would be impossible to grow such bush covers along with creeping covers without the bushes being overwhelmed by the creepers; the bushes alone would not give adequate protection against soil erosion on steep slopes. Moreover, bush covers would not stand being lopped for green manure as did the creepers, and they were likely to "indicate" other root diseases as well as those dangerous to rubber, and thus waste pest gang labour. In a comparison of bush covers and creeping covers for young rubber in Malaya, NAPPER (1940) found the incidence of infection to be higher by a third on the area under creeping cover; from the point of view of root disease treatment, however, creeping covers were more economical, on account of the additional cost of treating the infected bushes. Both as regards disease control and general requirements, therefore, creeping covers appear to be preferable to bush covers.

In North East India, TUNSTALL (1940) recommended that when

areas of old tea were being cleared for replanting, patches of vacancies and of infills should be marked off; on these patches, all the roots of both tea bushes and shade trees should be extracted as completely as possible. The remaining bushes might be dug out without taking any special care to remove all the roots from the soil.

*Chapter 14*

# CONTROL OF ROOT DISEASE IN PLANTATION CROPS: SPECIAL PROBLEMS

In the development of methods for control of root disease in plantation crops, an outline of which has been given in the two preceding chapters, primary emphasis has been laid upon eradication of the sources of infection. In the earlier days of plantation pathology, the complete removal of all buried timber from the plantation site before planting up was sometimes advocated, but this was generally admitted to be a counsel of perfection. A revolutionary change in methods of root disease control was brought about by NAPPER (1932-34) at the Rubber Research Institute of Malaya when he proposed that eradication of root disease fungi should be carried out under the young plantation crop, instead of before planting; a great economy in labour was effected by this new routine treatment, inasmuch as excavation was limited to actual instead of potential sources of root infection. A further advance was made by LEACH (1937) in Nyasaland, when he demonstrated that the development of many potentially dangerous sources of infection after felling of the jungle could be prevented by ring-barking the jungle trees well in advance of felling. LEACH's discovery was followed by NAPPER's (1939-40) development of the tree and stump poisoning methods in Malaya for the same purpose.

The amount of space thus far devoted to a description of these sanitation methods reflects their relative importance to the plantation grower. The usefulness of soil fungicides for root disease control in plantations is strictly limited, though such fungicides may sometimes be used in conjunction with other control methods, as in the employment of copper sulphate solution by NAPPER as described above (p. 112). Soil fungicides have also been used, though not with conspicuous success, in various attempts to eradicate root disease fungi introduced into "clean" areas (*see* below, p. 138). On the whole, however, phytocidal chemicals, such as the sodium arsenite used by NAPPER (1940) for stump poisoning in Malaya, and the heavy gas oil employed by SMITH (1932*b*) for destruction of banana stumps in Jamaica (*see* below, p. 136), are probably of more importance to the plantation grower than are fungicidal chemicals. TUNSTALL (1926) has emphasised the difficulties of eradicating root-infecting fungi ensconced within bulky pieces of timber buried at some depth in the soil by any method except that of excavation. Nevertheless, soil fumigation with carbon disulphide, applied through an injector, has given promising results in attempts at eradication of *Armillaria mellea* from the soil of Californian citrus orchards (THOMAS, 1938; THOMAS and LAWYER, 1939; GRIFFITH, 1941).

When choosing a site for establishment of a plantation crop, it is well to remember that some soils are more favourable than others for the development of a particular root disease. Some advantage of this fact has been taken in banana growing, following REINKING'S (1935) discovery that Panama disease (*Fusarium oxysporum cubense*) is more prevalent on soils of light texture; according to WARDLAW (1941), heavy alkaline soils are least favourable to the disease (*see* above, p. 45). Low-lying sites, unless properly drained before planting, will predispose a plantation crop to attack by such a parasite as *Sphaerostilbe repens,* the cause of violet root rot. Concerning the relation between incidence of root disease and soil conditions, less evidence is available for plantation crops than for field crops. Developments in the manuring of field crops have outstripped those in the manuring of plantation crops. Observations and experiments on the relation between manuring and incidence of root disease (*see* above, p. 54) have therefore been made almost exclusively on field crops; only few and casual reported observations, such as that of DE JONG (1933) concerning the slightly greater incidence of *Fomes lignosus* on rubber in manured plots, can be found on the relation between manuring and occurrence of root disease in plantation crops.

Certain root diseases, to which further space is devoted below, require special precautions or treatment for their prevention or cure. Such are the root diseases due to species of *Rosellinia,* which are favoured by a humid atmosphere and accumulation of humus, diseases due to fungi that are primarily wound parasites, such as *Ustulina zonata,* diseases in which root infection, by fungi like *Sphaerostilbe repens,* cannot occur in the absence of some such predisposing factor as waterlogging, and diseases, such as internal root rot of tea, formerly attributed to *Botryodiplodia theobromae,* in which fungi are purely secondary. These diseases, and the problem presented by the introduction of a root disease fungus into a "clean" area, are more fully considered below.

**Root Diseases Requiring Special Treatment:** — *Root diseases due to Rosellinia spp.* — The growth habit and parasitic activity of these fungi have already been described (pp. 50 and 61) ; it remains to discuss the special control measures appropriate to such a fungal growth habit. Little has been added to the recommendations made by NOWELL (1923) in the West Indies and by PETCH (1923) in Ceylon. Accumulations of dead leaves and other vegetable litter, which favour the saprophytic spread of these fungi, must be cleared away, leaving the ground, in PETCH'S phrase, "as bare as a tennis court." Ventilation should be improved by severe pruning of bushes or trees surrounding the diseased individual or group. As WATERSTON (1941) has pointed out, however, parasitic activity of *Rosellinia* is not confined to those

situations in which the fungus can make a rapid saprophytic surface spread amongst vegetable litter under dense shade and high rainfall; *Rosellinia* may occur as a parasite under conditions of lighter shade and lower rainfall, with little or no accumulation of surface litter. In the latter type of situation, spread of the fungus is more or less confined to movement along the roots of its host plants; such subterranean spread as a parasite is necessarily slower than the rapid surface spread as a saprophyte.. WATERSTON investigated the occurrence in such situations of a root disease due to *R. pepo* on cacao estates in Trinidad and Grenada, but was unable to correlate its incidence with soil reaction, or with organic matter, nitrogen, phosphate, or potash content of the soil. The disease occurred chiefly on soils of light texture — a limitation attributed by WATERSTON to the aeration requirements of the fungus.

*Charcoal root rot due to Ustulina zonata.* — The fungus causing this disease, which is well known on tea and rubber estates in Ceylon, and on rubber plantations in Malaya (PETCH, 1921, 1923; SHARPLES, 1936), spreads from plant to plant underground by root contact, in the same way as *Fomes lignosus, F. noxius* and *Ganoderma pseudoferreum*. *U. zonata* is also a well known stem parasite, gaining entrance through spore infection of wounds, so that certain special precautions must be observed when dealing with it. SHARPLES (1936) remarks that all authorities consider the collar to be the commonest seat of infection. Whereas in Java emphasis has been laid on infection through collar wounds made during changkolling (hoeing), in Malaya it is thought that accumulation of scrap rubber at the base of the tree provides suitable conditions for infection by *U. zonata,* through suffocation of the cortical tissue beneath such air-tight pads. Control measures should include prompt removal of felled rubber logs on which the fungus may develop as a saprophyte and later produce fructifications, periodical removal of scrap rubber accumulating at the base of the stem, and avoidance or adequate protection of wounds.

*Violet root rot due to Sphaerostilbe repens.* — Infection by this fungus can apparently occur only under certain soil conditions that lower the resistance of the roots; in Malaya, according to SHARPLES (1936), the disease is most frequently seen on rubber areas that have been flooded. TUNSTALL (1940) remarks that violet root rot is usually associated with badly aerated, stiff soils in the tea plantations of North East India. In exceptionally sticky soils, single lines of good plants may sometimes be seen along the edges of drains, with the intervening bushes poor and most of them severely attacked by *S. repens.* TUNSTALL also observes that excessive defoliation of the tea bushes through plucking and pruning may lead to such a lowering of the vitality of the roots that *S. repens* can effect entry; on the

lighter soils, the place of *S. repens* is taken by *Botryodiplodia theobromae.*

In the British West Indies, *S. repens* is commonly associated with a condition known as red root disease of limes; BAKER (1938), who has reviewed the history of this disease in the British West Indies, has concluded that the status of *S. repens* as a primary root parasite of limes is still unproven. He has recommended the budding of limes on sour orange root-stocks, which are resistant not only to the red root disease, but also to gummosis.

*Internal root rot of tea, formerly attributed to Botryodiplodia theobromae.* — Ideas concerning this "disease" of the tea bush were revolutionised by GADD (1928-1929*b*), who demonstrated that infection by *B. theobromae* was a secondary phenomenon, and that the "disease" was really caused by cultural practices. Internal root rot was stated by GADD to occur in Ceylon chiefly at middle and low elevations, where the plucking rounds were most frequent, and the pruning cycle the shortest; it was manifested as a failure to make fresh growth after pruning, and by subsequent death of the bush. GADD showed that failure to recover after pruning appeared invariably to be associated with absence of starch reserves in the roots, and that this condition actually *preceded* infection by *B. theobromae.* Lack of starch reserves thus appeared to be the cause, and the subsequent general infection of the weakened roots by *B. theobromae* merely an effect of the disease. In tea grown at the higher elevations, where assimilation could better keep pace with growth, the disease was almost unknown. GADD also observed that whereas roots infected by *B. theobromae* were completely deficient in reserve starch, those infected by *Poria hypolateritia, Rosellinia* spp., and *Ustulina zonata* showed a normal starch content. This rather constant association of infection by *B. theobromae* with low starch content of the roots is a phenomenon of considerable mycological interest, especially in connection with the findings of LEACH (1937) in Nyasaland (*see* above, p. 115). TUNSTALL (1940) in North East India agreed that susceptibility to internal root rot was almost always associated with lack of starch reserves, which might also be occasioned through defoliation due to drought or attacks of Red Spider. Of especial interest is his observation, cited above, that the roots of trees weakened through defoliation were infected by *B. theobromae* in light-textured soils, but in the heavier soils by *Sphaerostilbe repens.*

**Eradication or Immobilisation of an Introduced Root Disease Fungus:** — No better commentary can be given upon the problems involved in eradication or immobilisation of an introduced root parasite in a plantation crop than by recounting the story of Panama disease of bananas in Jamaica, full particulars of which have been

given by COUSINS and SUTHERLAND (1930) and by SMITH (1932*a*). The disease was identified on the Island early in 1912, and two more outbreaks, in widely separated localities were discovered soon afterwards. These outbreaks, considered to be of independent origin, were attributed to plantation labourers returning from the diseased banana lands of Central America, and bringing back infected tools and planting material, in spite of strict watch for such practices on the part of customs officers and plant quarantine inspectors. The Jamaican Department of Agriculture suspected from the first that Panama disease spread from one plant to another by root contact rather than directly through the soil; COUSINS and SUTHERLAND very aptly described this mode of spread as "chain action". A drastic Quarantine Regulation was therefore drafted in 1912, whereby all plants within one-chain radius of the original diseased plant had to be removed and destroyed, making a quarantine area of four square chains around the site of each diseased plant; the quarantine area was not to be replanted with bananas. The selection of a one-chain (22 yards) radius was based on the finding that the longest roots of a banana plant did not extend for a radius of more than half a chain (11 yards). In proof of the correctness of the original assumption that the disease spread by "chain action" along the roots of the plants, COUSINS and SUTHERLAND cited as an example plots rogued by this method in 1915, where in 1930 healthy bananas still surrounded the original quarantined areas. This was considered to disprove the assertion that the causal fungus, *Fusarium oxysporum cubense,* could travel independently through the soil in the absence of the banana plant. The loss of all the healthy plants on an area of four square chains was a heavy one to the planter, in spite of compensation, and with increase in incidence of the disease in any locality, a compromise was eventually made between economic considerations and the requirements of the rogueing treatment. Under a Panama Disease Order of 1925, a graded reduction in the quarantine area was permitted, as follows. For the first three cases on any property, an area of four square chains was to be enforced, for the fourth and fifth cases, one square chain, and after the fifth case, an area of half a square chain was to be quarantined. Thereafter, with approval of the Director of Agriculture, the quarantine area might be reduced to that of the "nine root system", whereby only the eight healthy plants surrounding each diseased one had to be removed and destroyed. COUSINS and SUTHERLAND remarked that experience had shown the rate of spread of the disease to increase with each relaxation of the quarantine restriction. SMITH (1932*a*) confirmed this conclusion, and stated that the quarantine regulations had met with success at least in checking the rate of spread of Panama disease. The "one root system", whereby the diseased plant alone was removed and destroyed, was to be deprecated as very dangerous,

and permissible only when the property was officially gazetted as infected, and adjacent lands were not endangered.

At about this time, a considerable improvement in the method of disposing of the plants to be destroyed was introduced by SMITH (1932*b*). According to the method originally adopted, the diseased plant was dug up and burnt immediately; the surrounding healthy plants were dug up, chopped into small pieces and heavily treated with lime. The area so treated was then fenced in, and maintained in quarantine. Apart from the difficulties and expense involved in destruction of banana plants by this method, there was the danger attendant upon moving soil, especially on river banks and steep slopes liable to wash. SMITH therefore sought for a method of killing the stumps of the felled plants *in situ;* many chemicals were tried, of which *heavy gas oil* (the fraction from the "topping" process of refining) proved most satisfactory in all respects, including that of cost. Only 2-3 pints are required per stump; after clearing away surface trash, the oil is applied around the stump, rather than on the cut surface. Oil so applied penetrates to the underground buds and kills the "eyes", from which new growth would otherwise start; large applications of oil to the cut surface of the stump were found to be quite unnecessary. An indirect benefit resulting from this method, by which sucker growth from the stumps is eliminated once and for all, has been pointed out by SMITH: "It has been found in the past that the adventitious suckers growing in a quarantined area have an extraordinary fascination for the small settler, who appears to prefer obtaining his planting material from such dangerous areas."

Unfortunately for the strenuous and well-directed efforts of the Jamaican Department of Agriculture, however, rogueing could prevent only the active spread of the wilt fungus, and could not stop other modes of dispersal. From the beginning, according to SMITH (1932*a*), the effectiveness of the quarantine operations was vitiated by non-cooperation on the part of some of the planters, more particularly small-holders, who not only failed to report infections, but carried out the unauthorised one root treatment on their own. In efforts to discover a "cure" for the disease, certain individual planters carried out all sorts of secret experiments on their own land, generally without taking proper precautions against the spread of infection. Diseased material was sometimes burnt, but might even be thrown into an adjacent stream, to avoid detection! Small settlers, again, had been known to plant up a new area with diseased banana suckers obtained from adventitious growth on quarantined land. One of the most effective agencies for passive spread of *Fusarium oxysporum cubense* had been that of flood and river water. SMITH considered that dissemination of the fungus by surface wash from local flooding after heavy rains was of particular importance; another dangerous practice

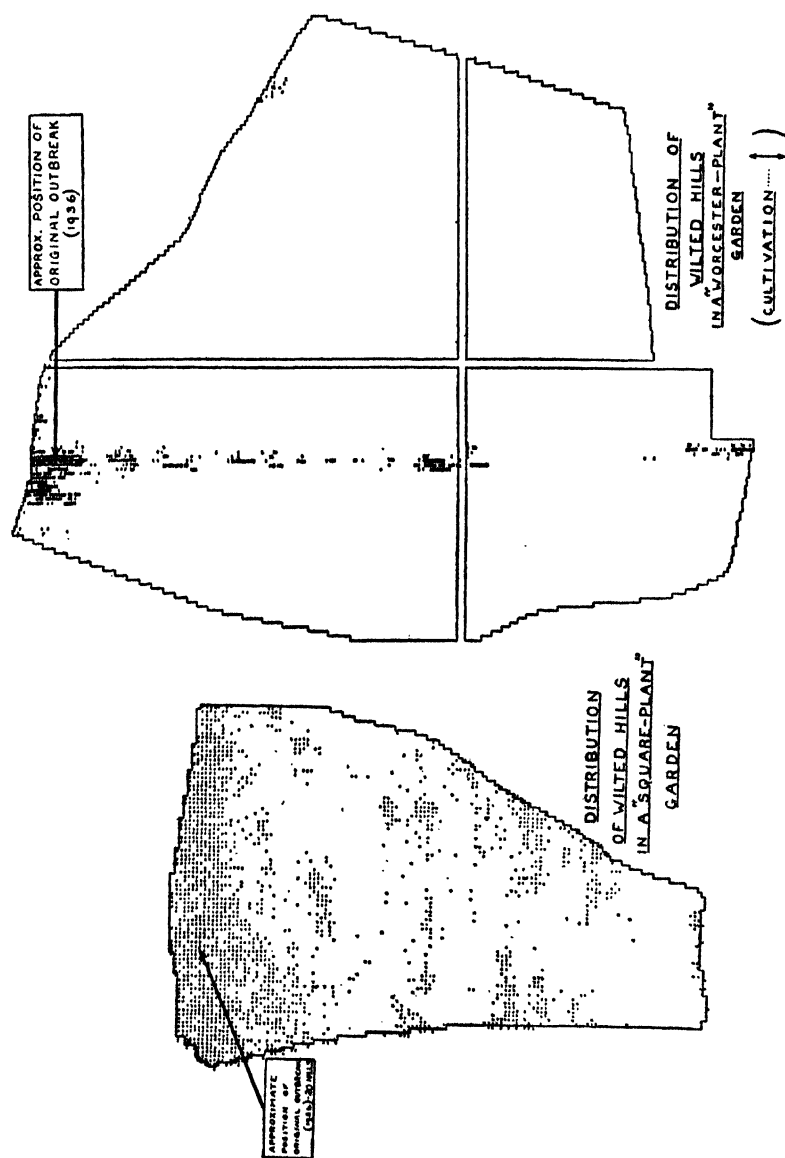



FIGURE 9. — Maps showing spread of *Verticillium* wilt of hops in "square-plant" garden, cultivated both up-and-down and across, and in "Worcester-plant" garden, cultivated up-and-down only. (*After W. G. Keyworth*).

was that of planting bananas right up to the banks of rivers bordering plantations. Finally, after commenting upon the loss to banana cultivation of large areas of the best alluvial soils in the river valleys and level lands, due to flood dispersal of the wilt fungus, SMITH (1936) reported the decision of the Department of Agriculture, taken in 1935, to permit one-root treatment of the disease throughout the Island.

An apparently introduced root disease that has recently caused considerable concern in the English hop industry is the wilt due to *Verticillium albo-atrum*, which has been investigated by KEYWORTH (1942). Whatever the origin of this disease may have been, its subsequent devastating spread in a number of hop plantations was not properly anticipated, with the result that insufficiently stringent measures were taken for eradication of the parasite. KEYWORTH has now given the following directions for eradication of a small outbreak of this disease in a new plantation: "Cut down and burn all the bines of diseased plants and *treat every adjacent plant similarly*. Then excavate a hole 1 yd. square and 1 yd. deep at each place where a treated plant has been and remove the soil from the hopfield. Pour 8 gal. of 2% formalin into and upon the walls of this hole and then fill with uninfected soil. Then treat the whole area where plants have been removed with 8 gal./sq. yd. of 2% formalin, retaining this with a bank if necessary. The spaces may be replanted after 3-4 weeks, but the young plants and surrounding old plants should be observed for wilt during the next season, and the procedure should be repeated if any wilt is seen."

This wilt disease of hops certainly presents unusual obstacles to the successful application of the usual routine measures of plant sanitation. KEYWORTH found that the fungus eventually reached all parts of badly diseased bines except the bracts and bracteoles of the hop cones. Such diseased bines were found to be dragged all over the hop plantations by the tines of the cultivators; this fact was considered by KEYWORTH to explain differences in spread of the disease in "square-plant" hop gardens with cross cultivation, and in "Worcester-plant" gardens with one-way cultivation. KEYWORTH also experimentally demonstrated that diseased leaves could act as inoculum, and might thus further the spread of the fungus to other parts of the same field, to other fields on the same farm, and even, perhaps, to other farms.

*Chapter 15*

# CONTROL OF ROOT DISEASE IN GLASSHOUSE CROPS

The control of root diseases of crops under glass presents problems similar in broad outline to those encountered in field crops; the control measures may similarly be classified under the three heads of crop rotation, plant sanitation, and checking of disease development in the growing crop. The relative importance of these three groups of control measures under glass is, however, very different to that under field conditions. Whereas in the field, crop rotation is of paramount importance in root disease control, in the glasshouse its scope is limited by high overhead costs, and consequently restricted choice of suitably remunerative crops. Another factor limiting the choice of crops for rotation is that of glasshouse design; a house ideal for tomato culture is less suitable for the raising of cucumbers, which require a higher temperature for optimum growth.

Under glass, the most important control methods are those comprised within the general term of plant sanitation. The greater value of the crop under glass permits of closer attention to individual plants than is economically possible in the field; where plants are grown in pots, raised beds, or otherwise in individual containers or compartments, the practice of rogueing, with appropriate disposal of infected soil and plant residues, is likely to be more effective than where plants are grown directly in the ground. Moreover, the more rapid growth of crops under glass, together with the greater opportunity for dispersal of parasites during cultural operations, necessitates a stricter attention to the principles of plant sanitation; especially is it important to avoid introduction of parasites either with the seed, or in infected propagating material, such as cuttings, etc. By far the most important control measure to be included under the heading of plant sanitation is that of partial sterilisation of the soil, or "soil sterilisation", as it is commonly though inaccurately called. Methods of partial sterilisation are described in detail below; they form the basis of root disease control in glasshouse crops.

The checking of root disease development by modification of the soil or aerial environment of the growing crop should theoretically prove more feasible under glass than out in the field. Nevertheless, the requirements of the growing crop for optimum vegetative and fruiting development must often conflict with the tentative recommendations of the plant pathologist for root disease control. Just as the efficiency of crop rotation for control of root disease in field crops has been responsible for the still-birth of many ingenious but less simple control methods, so the efficiency of partial sterilisation of the soil has had a like effect under glass. Although soil moisture content,

for example, is directly controlled by the glasshouse grower, little practical advantage is taken of this possibility for root disease control. Greater use is made by growers of their control over soil and air temperatures. By BEWLEY's (1922) method of controlling the *Verticillium albo-atrum* wilt of tomatoes through raising glasshouse temperature to at least 25°C., a spectacular "cure" of this disease can be effected. BEWLEY (1923) gives the following directions for control of the disease in this way: "As soon as the wilt appears and it is proved that *Verticillium albo-atrum* is the pathogen, the average temperature of the houses should be raised above 25°C. by suitably increasing the boiler heat, regulating the ventilation, and by closing down the houses from two to four hours in the middle of the day. A light dressing of whitewash on the glass makes the conditions still more favourable for the plants. As little water as possible should be given to the roots, as heavy watering merely aggravates the wilting, but a light overhead damping helps the wilted plants to recover. The plants should be encouraged to make fresh roots above the original diseased ones by placing fresh soil round the base of the plant." BEWLEY records that, in one nursery where these control measures were carried out, the percentage of wilted plants was reduced from 68 to 10 in a fortnight.

Another advantage enjoyed by the glasshouse grower over the farmer lies in his greater degree of control over soil composition. Glasshouse crops are often grown not in the original soil itself, but in an artificial soil or compost. Even if the original soil is employed, the heavy dressings of organic manures and artificial fertilisers commonly applied in glasshouse practice may rapidly change its physical texture and chemical composition. In the making of composts, a bewildering variety of "recipes" was formerly employed by professional gardeners; the number of composts in use by some of these artists approached the number of plant species under cultivation. Order and simplicity have recently been introduced into the practice of compost making by LAWRENCE and NEWELL (1936, 1941). The prime ingredients for a compost have almost invariably been loam, leaf-mould or manure, and sand. The leaf-mould or manure supplied both the organic matter for production of the desired texture in the compost, and some at least of the essential plant nutrients. Owing to the wide variation in composition of these organic materials, according to their original constitution and degree of decomposition, it has been impossible to produce a standard compost from such components. LAWRENCE and NEWELL achieved standardisation by discarding these dual-purpose organic materials, and employing peat as the source of humus. The manurial value of peat is relatively low, and does not fluctuate widely within any one type of peat; the physical properties of peat make it a more desirable constituent of compost than leaf-mould or

manure. As a result of their experiments, LAWRENCE and NEWELL proposed formulas for two composts, suitable for seeds and for potting, respectively: —

| | *Seed compost* | *Potting compost* |
|---|---|---|
| Medium loam ..................... | 2 volumes | 7 volumes |
| Peat ............................ | 1 volume | 3 volumes |
| Coarse sand ..................... | 1 volume | 2 volumes |

LAWRENCE and NEWELL found these composts suitable for growth of a wide variety of glasshouse plants, when used in conjunction with a balanced mixture of artificial fertilisers (for which they supplied a formula), together with chalk. Standardisation of the compost, as recommended by LAWRENCE and NEWELL, may prove useful in the solution of certain root disease problems as well.

DUNLAP (1936) has suggested that control of damping-off in seedling pans might be achieved more easily by raising seedlings in quartz sand moistened with a nutrient solution than in partially sterilised soil, wherein a re-introduced damping-off fungus may spread with especial rapidity. An example of an extreme development in this type of root disease control is afforded by the commercial culture of glasshouse crops in tanks of nutrient solution (GERICKE, 1940).

After this brief general account of root disease control in crops under glass, more detailed consideration may now be given to partial sterilisation of the soil, which is as important to the glasshouse grower as is crop rotation to the arable farmer.

**Partial Sterilisation of the Soil:** — This is by no means a new practice. By partial sterilisation is meant any treatment of the soil by heat, chemicals or other agent, whereby the soil microflora and fauna are reduced and simplified. One object of partial sterilisation is to kill all disease-producing micro-organisms and insect pests, whilst leaving alive at least some of the beneficial soil micro-organisms; the spore-forming bacteria usually escape destruction, and the more common non-sporing forms are re-introduced and re-establish themselves with little delay. Partial sterilisation produces not only microbiological but also physical and chemical changes in the soil; a notable effect of heat treatment is the liberation of plant nutrients, especially nitrogen, in an available form through breaking-down of complex organic compounds. Partial sterilisation by heat, in particular, may also improve the physical structure of the soil; according to NEWHALL (1935), the water-holding capacity of the soil may be lowered by steaming, but this is not necessarily a disadvantage.

The history of partial sterilisation, together with its modern applications, has been discussed by WAKSMAN (1931), NEWHALL *et al.*

(1934), NEWHALL (1935), RUSSELL (1937), BEWLEY (1939) and MARTIN (1940). The increase of crop following a fire over the soil was well known to the ancients; such improved growth has usually been attributed to the high potash content of the wood ash, but a liberation of nitrogen through heating of the surface soil must also occur. Concerning pioneer farming in the early days of the U. S. A., NEWHALL *et al.* (1934) write: "In newly-cleared land, places where brush piles were burnt dotted the fields. The early settlers learnt that delicate plants like watermelons, muskmelons, and even beans, could be grown in these spots where they would damp-off otherwise." It is not surprising to find that authors disagree concerning the credit to be given for the "discovery" of the benefits of partial sterilisation. On this point, MARTIN (1940) remarks: "The first observations of the increase of yield following partial sterilisation were made independently by GIRARD (2)* and by OBERLIN (3)* in 1894. These workers had employed carbon disulphide as their sterilising agent. Similar results were found after the application of other volatile antiseptics, and in 1907, DARBISHIRE and RUSSELL (4)* showed that partial sterilisation by heat produced a like result." WAKSMAN (1931), however, has drawn attention to an earlier paper by FRANKE (1888), who correlated the increased crop growth observed to follow heating of soil with enhanced solubility of soil mineral constituents and organic matter.

Much was done by RUSSELL and his collaborators (*see* RUSSELL, 1937) in their investigation of the complex causes of soil sickness in English glasshouses; concerned in bringing about this condition were not only parasitic fungi, nematodes, and insect pests, but also a deterioration in the physical and chemical condition of the soil through repeated heavy dressings of artificial fertilisers and continual heavy watering. BEWLEY (1934) has since shown that the last evil can be combatted by incorporating layers of fresh straw with the soil. Whatever the causes of soil sickness, however, the cure advocated by RUSSELL and his co-workers in England proved such a success that partial sterilisation of the soil has become a routine measure in English commercial glasshouses. Although credit has probably been justly assigned to these investigators, inasmuch as the widespread adoption of partial sterilisation was due largely to their efforts, yet it appears that steaming of the soil was first tried out in the U. S. A. at a still earlier date. Thus NEWHALL (1935) states: "The first use of steam for commercial greenhouse soil sterilisation seems to have been made in 1883 by W. H. RUDD in Greenwood, Illinois. He laid three steam pipes perforated at 18-in. intervals in the bottom of a wooden bin 4½ ft. deep and holding 480 cu. ft. of soil."

Complete sterilisation of the soil, on the other hand, is not bene-

* GIRARD (1894), OBERLIN (1894), DARBISHIRE and RUSSELL (1907).

ficial but harmful; in addition to extinction of all beneficial, as well as harmful, soil micro-organisms, there is a loss of soil organic matter, and often a marked deterioration in soil structure, or tilth, as well. This may happen when dry heat is used as an agent for partial sterilisation as in baking, or in using the "New York type" of electric partial steriliser with soil insufficiently moist. Concerning this possibility, BEWLEY (1939) observes: "When baking a soil, it is possible to overheat it, especially if the soil is on the dry side, and, when this occurs, the soil becomes 'dead' and will not support plant growth. Seedlings planted in it turn blue and hard, and grow very slowly, if at all."

Methods of partial sterilisation at present in use may be classified as follows: —

(*a*) by heat (i) steam,<br>
(ii) baking,<br>
(iii) electricity,<br>
(*b*) by chemicals.

*By steam.* — This is by far the most effective agent for partial sterilisation as yet discovered; unlike dry heat, it can be used to treat the soil *in situ* in the beds. It has the advantage over all chemical agents so far tried of being equally lethal to parasitic micro-organisms, including plant-infecting nematodes, to insect pests, and to weed seeds. Various contrivances have been designed for the steaming of relatively small quantities of loose soil, intended for the filling of pots, flats and seedling pans, etc. The chief practical interest centres, however, in methods of steaming soil in the beds, of which a brief description may now be given.

In the *buried tile method,* a system of 3-4-inch diameter clay drainage tiles is laid 13-16 inches deep in rows 18 inches apart, in permanent position in the beds (NEWHALL *et al.,* 1934). When steaming is to be carried out, the system is connected up to the boiler; the steam escapes into the soil from the cracks between the tiles. According to NEWHALL *et al.,* such tile systems may be expected to last for at least 12-15 years without resetting. An additional advantage accruing from such a buried tile system is the use to which it can be put either for sub-irrigation, or, in conjunction with flooding, for the leaching of an excess of soluble salts out of the soil. Although apparently popular in the U. S. A., the tile method of steaming is little used in England, and no mention of it is made by BEWLEY (1939).

In the *buried perforated pipe method,* perforated pipes are laid in parallel trenches 6-18 inches deep, and at a distance apart depending on the depth, and covered with soil. One end of each pipe is connected by an elbow to a short upright pipe, through which the live steam is conducted into the buried perforated pipe. In England, where this system is known as the "Hoddesdon", the horizontal perfo-

rated pipes are customarily 6-7 feet long (BEWLEY, 1939), but in the U. S. A., they may range from 20 to 120 feet (NEWHALL *et al.*, 1934). Whilst soil steaming is proceeding through one set of parallel pipes, the workmen lay another set in position. A variant of the buried perforated pipe method employed in England is the *small grid method;* horizontal perforated pipes 2-2½ feet long and 10-12 inches apart are connected at their proximal ends to a cross pipe 8-10 feet in length. The apparatus thus resembles a comb, built-up out of tubes.

By the *steam harrow method,* which is sufficienty described by its name, the labour required for steaming, and consequently the cost of the operation, is much reduced. The effect produced is more superficial, however, and the method is not considered suitable for heavy soils. The *inverted steam pan method,* which in England is known as the *tray method,* is similarly characterised by lower labour costs, and by a reduced effective depth of working; it is therefore especially suitable for the treatment of seed-beds and raised benches, where depth of soil is limited. Various mechanical contrivances for moving the heavier types of pan are in common use. NEWHALL (1939) has recently described an electrically heated inverted steam pan devised at the Cornell Agricultural Experiment Station; steam is generated by electric strap heaters operating in troughs of water placed inside the inverted pan.

Certain precautions are essential to success in the use of all these steaming methods alike. The steaming must, of course, be thorough and must be effective to a sufficient depth in the soil. To conserve heat, it is usual to cover the soil with sacking or other insulating material. The soil should be neither too wet nor too dry, if the best result from steaming is to be obtained; BEWLEY (1939) suggests that "generally speaking, a soil sufficiently dry for potting purposes is in a suitable condition for steaming". With such a suitable moisture content, optimum channels for conduction of the live steam are probably provided by the pore spaces of the soil. If the soil is too dry, the pore spaces are too wide, and the steam escapes before it has completed its work of partial sterilisation; if, on the other hand, the soil is too wet, then insufficient pore space is provided for thorough penetration of the steam to all parts of the soil. Moreover, if the soil is too wet, heat is wasted in raising the temperature of the excess soil moisture to boiling point, and the soil will also take longer to dry-out after steaming.

Further precautions, again, must be observed in the care and use of soil after partial sterilisation by steam. Steamed soil is a medium more favourable than unsteamed soil for the activity of most root-infecting fungi; nutrients are set free by the steaming, and the competitive effect of other micro-organisms is much reduced. For this reason, HARTLEY (1921) suggested that steamed soil should be

reinoculated with saprophytic micro-organisms before being used for the raising of seedlings. Especial care is therefore necessary to prevent contamination of steamed soil by untreated soil infected with one or more of the root parasites; the feet of workmen, for instance, may so contaminate the freshly steamed soil during the actual progress of steaming. BEWLEY and BUDDIN (1921) have shown that the glasshouse water supply may constitute an important source of infection (*see* above, p. 94). Where the soil beds are not separated from the subsoil, recolonisation of the beds by root-infecting fungi is only a matter of time, since the subsoil serves as a reservoir of infection, which may be tapped by the roots of the first crop grown in the steamed soil. Under such conditions, therefore, periodical soil steaming, like crop rotation, serves not so much to eliminate root parasites as to restrict the damage that they do, and keep it at a commercially unimportant level. Where such spread of a root-infecting fungus from infected subsoil is especially rapid, however, the culture of plants in raised beds or benches, which can be treated *in toto,* may be adopted, as recommended by WICKENS (1935) for control of the *Verticillium cinerescens* wilt of carnation.

A further, though temporary, disadvantage of steamed soil is its toxicity to most seedlings, and to delicate plants; the effect is least noticeable with robust and "strongly feeding" plants like the tomato. Steaming, or other heat treatment, is well known to increase the content of soil solutes very considerably; the concentration of solutes increases with the duration and intensity of the heat treatment. JOHNSON (1919) demonstrated that the toxicity of steamed soil to seedlings was due chiefly to the ammonia produced through the heating. The toxic effect is greater in rich soils with a high organic content than in poor soils; it is increased by addition of chalk or lime to the soil before steaming (LAWRENCE and NEWELL, 1936). In the past, it has been deemed inadvisable to use steamed soil sooner than 3-6 weeks after steaming; alternatively, ammonium salts could be leached out of the soil by flooding at least once with water — a wasteful procedure. A better alternative is that of applying a sufficient dressing of superphosphate to the steamed soil to balance the excess of soluble nitrogen; this valuable effect of phosphate in combatting the ammonium toxicity in steamed soil seems to have been discovered by LAWRENCE and NEWELL (1936, 1941).

*By baking.* — Methods of baking soil by dry heat have been described by NEWHALL *et al.* (1934) and, in greater detail, by BEWLEY (1939). They are suitable only for relatively small quantities of soil, and cannot be used to treat soil *in situ* in the beds, as in steaming. If the soil is too dry when treated, there is danger of overheating, with resulting loss of organic matter, and, in the extreme instance, with complete sterilisation.

*By electricity.* — The use of electricity to effect partial sterilisation of the soil was apparently first reported by ELVEDEN (1921) in England, but further development of this method is due almost entirely to American investigators, whose work has been summarised by NEWHALL and NIXON (1935). Two types of electric partial steriliser have been developed; in the Ohio type, the soil is heated directly by passage of a current through the soil from one electrode to another, whereas in the New York type, the soil is indirectly heated by passage of a current through metal heating elements. In the Ohio type of partial steriliser as well as in the New York type, the soil is partially sterilised by the heating action of the current, and not by the wave effect. Both types of partial steriliser have so far taken the form of containers designed for treatment of limited quantities of loose soil; no satisfactory method for effecting partial sterilisation of soil in the beds seems so far to have been reported, although various attempts have been made to solve this problem. According to NEWHALL and NIXON, uneconomic lengths of heating element would be required for use of the New York method in this way, whereas use of the Ohio method is complicated by the difficulty of getting satisfactory plate to soil contacts in the uncompressed soil of the beds, by the development of uneven temperatures, and by leakage of power, with attendant personal risk to the operator. If these difficulties can be overcome, electricity may eventually compete with steam as a method for partial sterilisation of soil *in situ*. An interesting new machine for continuous partial sterilisation of loose soil has been described by NEWHALL (1939); approximately 7 cubic feet of soil, or enough to fill 18-20 flats, is turned out in an hour by this machine, the principle of which is similar to that of an electric baker's oven.

For satisfactory partial sterilisation by electricity, the soil must be at a suitable moisture content. If it is too dry in the New York container, it becomes overheated, with consequent loss of fertility, around the heating elements. With the Ohio method, electrical conductivity of the soil is too low for effective heating below a certain limiting moisture content; for this reason, overheating of the soil is impossible, as the current is reduced to zero as soon as the soil starts to dry out. The electrical conductivity of quartz sand, as used for propagating benches, is too low for satisfactory partial sterilisation by the Ohio method, but this difficulty may be overcome, according to NEWHALL and NIXON, by addition of 0.5% potassium nitrate to the sand before treatment. Similar conclusions concerning the relation between electrical conductivity of the soil and its moisture and salt content were expressed by VAN DER MUYZENBERG and VAN RIJN (1936), from their experimental application of these American methods in Holland.

*By chemicals.* — For partial sterilisation of the soil with especial

reference to the need for controlling root-infecting fungi, the performance of formaldehyde is at present outstanding; the consideration of other chemicals for this purpose is at present probably a waste of time. As an agent for general purpose partial sterilisation, formaldehyde, like all other chemicals upon which report has thus far been made, is inferior to heat; it is ineffective against nematodes, insect pests, and most weed seeds, and is less lethal to fungal sclerotia than are the heat treatments. On the other hand, it is a cheap chemical, and has exceptional penetrating power; HUNT *et al.* (1925) demonstrated that its penetration was equal to that of the water carrying it in solution. Concerning rate of application, NEWHALL *et al.* recommended that one gallon of formalin (40% formaldehyde in aqueous solution) be diluted to 50 gallons with water, and that half a gallon of the dilute solution be applied per square foot of soil surface. BEWLEY (1939) recommended a solution of the same dilution, to be applied at either of two rates, which work out at half a gallon per 0.9 square foot and per 1.62 square foot, respectively. He suggested that the soil should be turned over one spit deep after treatment, on the same day. NEWHALL *et al.*, on the other hand, directed that the soil should be covered for a day or two after treatment in order to retain the fumes of formaldehyde for as long as possible. An interval of 14 days after treatment is usually deemed sufficient for dissipation of the gas; after this, the soil can safely be planted. Effective as formaldehyde is by comparison with other chemicals for partial sterilisation, it cannot compete with steam where this is available. Some interesting crop returns have been quoted by BEWLEY in a comparison of the yield of tomatoes following treatment of the soil by steam, formaldehyde, and cresylic (carbolic) acid; yields of fruit were 51, 45, and 40.25 tons per acre, respectively, as compared with a yield of 37.9 tons on the untreated control soil.

A method was devised by BEACHLEY (1937) for treating soil with a mixture of steam and formaldehyde vapour, by means of the inverted steam pan; the formaldehyde solution was vaporised by pumping it through a heated coil. The formaldehyde vapour was found to penetrate the soil as deeply as the steam; a deeper penetration was thus achieved than when formaldehyde was applied as a liquid drench. By using 1 lb. of formaldehyde per 100 square feet of soil surface treated by the combined steam and formaldehyde method, the necessary period of steaming could be reduced from 30 to 20 minutes, and the cost cut from 1 dollar to 80 cents per 100 square feet. Moreover, most of the vegetable and flower seeds that were tested germinated and developed satisfactorily when sown in soil treated only 24 hours previously.

Many other chemicals have been tested as agents for partial sterilisation, but none can compete with formaldehyde for cheapness and

fungicidal efficiency. The most promising, perhaps, is chloropicrin, which is an efficient insecticide (ROARK, 1934) and has been developed by GODFREY (1935) and his collaborators (GODFREY *et al.*, 1934) as a nemacide. GODFREY (1936) later showed that chloropicrin was a useful fungicide as well; it has since given encouraging results in the hands of other workers, when employed against a variety of soil-borne diseases, *viz.* black leg (*Moniliopsis aderholdi*) of cabbage (EZERSKAYA, 1937), black root rot (*Thielaviopsis basicola*) of tobacco (GROOSHEVOY *et al.*, 1940), wilt (*Fusarium bulbigenum* var. *lycopersici*) of tomato (YOUNG, 1940), foot rot (*Rhizoctonia solani*) of annual stocks (DIMOCK, 1941), southern sclerotial rot (*Sclerotium rolfsii*) of sugar-beet (DAVEY and LEACH, 1941), clubroot (*Plasmodiophora brassicae*) of crucifers and other diseases (HOWARD, 1940). Adequate confinement of the chloropicrin vapour is essential for successful use of this fumigant; for this purpose GODFREY (1934) developed a glue-coated paper as a soil cover, with which GODFREY *et al.* (1934) obtained improved nematode control.

Non-persistence in soil is an essential quality for any chemical to be used in wholesale partial sterilisation of glasshouse beds. This requisite eliminates many chemicals of proved fungicidal efficiency, such as the salts of copper and mercury; for the same reason, sulphur and sulphuric acid are unsatisfactory as a substitute for formaldehyde. The only chemicals likely to be adopted by the glasshouse grower for routine partial sterilisation are those that give a substantial temporary increase in soil fertility, in addition to destroying parasites and pests.

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# GENERAL INDEX

# AUTHOR INDEX